

**Ecology of a hedgehog *Erinaceus
europaeus* population in southern
Sweden**

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ABSTRACT

A hedgehog population in southern Sweden was studied between 1972 and 1980. Population sizes varied between 23 individuals (1972-1974) and 53 (1978). No captured subadult female was found to have suckled young. Recruitment rate (average 2.8 young/adult female) was not correlated with non-juvenile densities, but some features of delayed density-dependence were recorded. The annual mortality averaged 47 % for non-juveniles and 34 % for juveniles. Most mortality occurred during the winter. For non-juveniles, winter mortality was correlated with non-juvenile densities and it was also correlated with winter temperature. This was not found for juveniles. Summer mortality averaged 15 % and traffic kills was the predominant cause of death. The animals killed were mainly non-juveniles. In conclusion, the hedgehog population appeared to be more influenced by environmental factors than by density-dependent factors. The hedgehog did not show any territorial behaviour. No spatial separation between the home-ranges was found. Hedgehogs feed mainly on invertebrates, which occur as a patchy food resource, influenced by habitat structure and microclimate. This forces the hedgehogs to move around in search for food. It makes it difficult for male hedgehogs to predict the location of female hedgehogs and the defence of home-ranges uneconomical. The adult male moved extensively during mating period in search for females. The males lost in weight during the mating period, which reflects the male's effort expended in searching for females. Mate guarding occurred only in connection with courting and mating. In comparison with searching behaviour, guarding a single female would be disadvantageous for a male due to the long time expended in one female and the loss of mating opportunities with other females. In summary, the mating system of the hedgehog appears to be a case of overlapping promiscuity governed by the temporal and spatial dispersion of the food resources and the solitary habit of the female, giving searching and promiscuous behaviour in males an advantage over other alternatives.

List of papers

This thesis is based on the following papers:

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|-----|---|----|
| I | Distribution of the European hedgehog (<i>Erinaceus europaeus</i> L.) in Sweden and Finland.
(Ann. Zool. Fennici 18: 115-119, 1981) | 11 |
| II | Demography and population dynamics of a hedgehog population in Sweden.
(Manuscript) | 19 |
| III | Young production of European hedgehog in Sweden and Britain.
(Acta Theriol. 34: 504-507, 1981) | 33 |
| IV | Home range size of the European hedgehog (<i>Erinaceus europaeus</i>) in South Sweden.
(Manuscript) | 39 |
| V | Spatial organization and mating system in a hedgehog population.
(Manuscript) | 51 |
| VI | Body weight changes in the European hedgehog.
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Preface

In the 1960-s people became concerned about the future and status of the hedgehog in Sweden. It was alleged that the traffic kills of hedgehogs was the main cause of a general decline of the hedgehog population in Sweden. It was also found that basic knowledge about hedgehog ecology was missing. In 1972, Görgen Göransson and Johnny Karlsson started to investigate a hedgehog population in Revingeby, south Sweden, and thereby initiating the following years hedgehog studies. Later on Anders Lindgren continued the project. Finally in June 1976, I took over the project with Sam Erlinge as my supervisor. Since 1981 I have been working with wild boars which may have prolonged and intensified the birth labor of the thesis. However, it has given me experience and bread for the day.

Various people helped me in my work. Some helped just by being my friends and unknowingly gave support that way. Others gave help in connection with the actual work. I am especially grateful to my supervisor Sam Erlinge whose interest and knowledge in ecology has been most helpful to me. Especially in later years Sam Erlinge gave me full support and showed great patience with me when I almost never did as he wanted me to do. For this I am very grateful. Sam Erlinge financed my field work by grants from National Swedish Environmental Protection Board and by grants from World Wild-Life Fund. The warm and friendly atmosphere in the Wildlife Research group also helped a lot in my studies (One might even say hot, eruptive and vulcanic atmosphere requesting a sergeant's voice).

Per Brinck, Head of the Department, is thanked for his assistance and help with the final draft of the thesis. I also thank Johnny Karlsson, Olle Liberg, Jon Loman, Sigfrid Lundberg, Ingvar Nilsson, Torbjörn von Schantz, Mikael Sandell who offered comments and criticism on various manuscripts. Ulla Holmberg is thanked for her assistance in our library and for translating a Russian paper into Swedish. Considerable assistance in the field was given by Jens Dahlgren, Boel Jeppsson, Thomas Madsen and Monica Osterkamp. Görgen Göransson constructed the radio-transmitters and gave technical advice and assistance on the radio equipment and his help is greatly appreciated.

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I thank Karin Lithner for her support as a dear and very close friend and for making life more fun. Last but not least, I thank my parents for their whole-hearted and loving support during the many years of studies. Without this support I question if this thesis ever had been written.

Summary of results

Although the hedgehog lives in close connection with man, little is known about its ecology. This thesis adds to our knowledge by providing basic information on various aspects of the ecology of a hedgehog population in southern Sweden.

The distribution of traffic kills indicates that hedgehogs are mainly found in connection with human settlements (Göransson et al. 1976). In farming and forested areas the density is much lower than in villages and suburban areas where hedgehogs often are found in large gardens, allotments and commons with hedges, bushy areas and lawns. Occasionally, hedgehogs are seen in city centers, but those animals have usually gone astray. Urban development might be a threat to the hedgehog (Morris 1966). Open spaces are built upon and old houses with large gardens are pulled down and the areas are rebuilt with houses with small gardens. In this way hedgehog habitats are reduced.

Why are hedgehogs abundant in suburban areas and in villages? There are suitable places for winter nests, compost heaps, hedges and sheds to nest in and offering protection from harsh weather, and there is abundant food, e.g. earthworms, slugs and snails. In Sweden, as in England, hedgehogs are regarded as free-living pets and people feed them. Potential predators, e.g. foxes and badgers, have a low density. A few factors such as traffic kills are on the negative side.

The hedgehog is a hibernating species. One important characteristic of such an animal is that activities as breeding and rearing young, foraging for maintenance and fat storing for the hibernation all have to be done during a short period of the year (Kalabukhov 1960). For comparison, I have separately considered two main periods of the year i.e. the season of activity (the summer half of the year) which includes the mating and the post-mating period, and the hibernation period (winter half of the year) (II and V).

Population dynamics

Population number changes primarily because of births and deaths, and, secondarily because of migration. The number of animals in the hedgehog population studied increased in the beginning of the study and stayed thereafter on about the same level, except in the last year of the study when the number decreased (II). Mean litter size in Sweden was calculated from enquiries and found to be 5.2 young per female (III). No captured subadult female was found to have suckled young, indicating a low reproductive rate in subadult females (II). The estimated number of recruited juveniles varied between the years. Recruitment rate was not correlated with subadult/adult densities, but some features

of delayed density-dependence were recorded. The fact that females normally do not breed until they are 2 years old may promote delayed effects on the hedgehog's population dynamics (II).

Most of the mortality occurred during the winter. The annual mortality varied greatly between years averaging 47 % for subadult/adult and 34 % for juveniles (II). For subadult/adult, winter survival was negatively correlated with subadult/adult densities (II). A low recovery rate of individuals between years (indicating winter mortality) has been observed also in populations of hibernating sciurids (for references see Michener and Michener 1977). For Richardson's ground squirrel (Spermophilus richardsonii) recovery rate varied between 6 % and 62 % in different studies. High losses were also reported for other sciurid species. In general, fewer juveniles than adults were recovered and fewer males than females. For the Alpine Yellow-Bellied Marmot (Marmota flaviventris) Johns and Armitage (1979) conclude that overwinter mortality is a significant source of population losses.

Hedgehogs put on weight considerably during the post-mating period preceding the hibernation by increasing the fat deposits (VI). The amount of fat is essential for survival during hibernation. Hedgehogs experience substantial weight loss during the winter season (II and VI). This appears to be a general phenomenon among hibernators. It has been reported for Spermophilus spp., Marmota flaviventris and Zapus princeps (Michener 1974, Armitage et al. 1976, Michener 1978, Boag and Murie 1981, Phillips 1981, Cranford 1983).

Weather and length of summer probably have an important influence on population density (II), as indicated also from studies in England and New Zealand. In my study, only subadult/adult mortality was correlated with winter temperature (II). Other factors such as winter nest quality and the ability to construct winter nests may be more important for juveniles than for subadult and adult animals.

Summer mortality averaged 15 % and traffic kills were a predominant cause of death at that time (II). Hedgehogs roam over large areas and have large home ranges (II and IV). The adult male hedgehog is very active during the mating period which coincides with high incidence of traffic kills. The females suffer more from traffic kills during the post-mating period (Göransson et al. 1976, 1978, Paper II and V). More males than females were killed, which may be a result of the former's larger home ranges (Göransson et al. 1978, Paper IV). A large home range means crossing more roads and crossing them more frequently.

Harestadt and Bunnell (1979) showed that there was a relation between body weight and home range. According to their formula the expected home range size for hedgehogs was 16 ha for adults, both males and females. My data show an average range size of about 47 ha for adult males and about 20 ha for adult

females (IV). The formula indicates a general relationship, but it does not take into account such things as different mating behaviour. The large home range of adult male hedgehogs is due to the male's search for females during the mating period (see below). Further, estimates of home range size vary considerably depending on the method used to calculate the size (IV).

Climate limits the distribution of the species in Sweden. In the northern part of the country the environment may be too harsh to allow a population to maintain itself without the help of man (I, II and VI). The summer may be too short to allow the young to grow up and to store enough energy for the long winter. Winter temperature may be so low that survival is severely hampered.

In conclusion, the hedgehog population studied appears to be more influenced by environmental factors than by density-dependent factors.

Spacing-out pattern and social organization

Ecological factors are important in shaping mating systems, spatial behaviour and partitioning of parental care between males and females (Krebs and Davis 1978, Krebs and Davis 1981, Wittenberger 1981). A fundamental aspect of theories on spacing strategies is that an animal should defend a territory when it is economically defendable (Brown 1964). No spatial separation between the home ranges were found and the hedgehog did not show any territorial behaviour (V). Hedgehogs feed mainly on invertebrates such as earthworms which occur as a patchy food resource, influenced by habitat structure and microclimate (Kruuk 1978, MacDonald 1980, Paper V). This forces the hedgehogs to move around in search for food. It makes it difficult for male hedgehogs to predict the location of female hedgehogs and the defence of home ranges uneconomical (V).

The adult males moved extensively during the mating period in search for females (V). While females did not loose weight during the mating period, male hedgehogs did, which reflects the males' effort expended on searching for females (V and VI). In general, if only the female lavish parental care and if the probability for a male of finding another mate is high, then promiscuity will be the male's best strategy. What polygynous system that will be developed depends on whether the net reproductive success associated with, e.g., guarding females is higher than that associated with searching and promiscuous behaviour (Rubenstein 1980). In hedgehogs mate guarding occurred only in connection with courting and mating (V). Because of the solitary habit of the female hedgehog it is difficult for a male to follow and guard her longer than it takes for courting and mating and there is always a risk of being forced away by another male. In comparison with searching behaviour, guarding a single female would be disadvantageous for a male due to the long time expended on one female and the loss of mating opportunities with other females.

Due to the different behaviour of the sexes and the fact that only females

rear young, different constraints will affect the sexes (V and VI). The adult male lost weight during the mating period suggesting that mate searching is highly energy consuming, while during post-mating period they increased their weight considerably due to fat deposition (V and VI). During the mating period adult females increased their weight slightly, while their weight increase during the post-mating period was less than for adult males (VI). For adult females, in contrast to adult males, the post-mating period is a time of great food demand connected with pregnancy and provisioning of food not only for themselves but also for the young via milk production (V and VI). In terms of energy demand during the period of activity, male hedgehogs seem to experience hardest strain during the mating period, whereas adult females face hardest strain during the post-mating period (VI).

In summary, the mating system of the hedgehog appears to be a case of overlapping promiscuity governed by the temporal and spatial dispersion of the food resources and the solitary habit of the females, giving searching and promiscuous behaviour in males an advantage over other alternatives.

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Paper I

Distribution of the European hedgehog (*Erinaceus europaeus* L.) in Sweden and Finland

Distribution of the European hedgehog (*Erinaceus europaeus* L.) in Sweden and Finland

Hans Kristiansson

Kristiansson, H. 1981: Distribution of the European hedgehog (*Erinaceus europaeus* L.) in Sweden and Finland. — Ann. Zool. Fennici 18: 115–119.

Information on the distribution and changes in abundance of the hedgehog in Sweden was collected by means of questionnaires. The investigation showed that man has influenced the distribution of the hedgehog in Sweden (as in Finland and Norway) due to intentional introduction. In Finland and Sweden, its range has expanded during the twentieth century. However, this has occurred much faster in Finland than in Sweden. At present, the hedgehog is found in most parts of southern and central Sweden, and in Norrland, along the coast up to the Finnish border. A "minimum time-span" was calculated to predict the areas in which the hedgehog is expected to be found in self-maintained populations. This time-span was calculated to 155 days and covers the time needed for reproduction, storage of energy and growth of the young. It corresponds rather well with the northern distribution limit of the hedgehog. It was found that no large-scale general changes in abundance occurred between 1975 and 1979.

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1. Introduction

It is widely believed in Sweden that the hedgehog population has decreased dramatically during recent decades. The hedgehog is reported to be near extinction in some areas and road mortality is often put forward as a major reason for this decline. However, recent investigations in southern Sweden indicate that the influence of road mortality has been exaggerated (Göransson et al. 1978).

The information on hedgehog distribution given in field guides and textbooks is based mainly on tradition and not on systematically collected information. The aim of this study is to provide more scientifically based information on recent distribution of the hedgehog in Sweden, and to analyse possible trends during the period 1975–1979. Comparable information is available from Finland (Kristofferson et al. 1966, 1977) and this report includes a comparison between Sweden and Finland.

2. Methods

Information was collected by means of questionnaires

which were sent to local societies associated with the Swedish Society for the Conservation of Nature and to all members of the Swedish Youth Federation for Environmental Studies and Conservation. I asked for information about the presence/absence of hedgehogs during the years 1975–1979, changes in abundance during this period, and any introduction of hedgehogs by man into the actual locality.

The hedgehog is a well-known animal in Sweden and is confined mainly to human settlements. I, therefore, consider the replies received as being reliable. Out of 17,000 questionnaires sent out about 900 were returned.

3. Results

3.1. Previous information on the distribution

Linné stated in his Fauna Svecica (1761) that the hedgehog was a rare animal in central Sweden (Svealand) but he gave no real information about the situation further to the north: in Norrlandia vix occurrat. Nineteenth century handbooks (Nilsson 1847, Lilljeborg 1874) state that the hedgehog is not uncommon in southern and central Sweden (Fig. 1); only one observation from Norrland is mentioned. In the beginning of the twentieth century, hedgehogs were found



Fig. 1. Approximate distribution limits of the hedgehog in Sweden during three periods: 1850: Linne 1761, Nilsson 1847, Liljeström 1881, 1920: Ekman, 1922, 1970: this investigation. The arrows indicate reports of transported and introduced animals. The year of introduction is shown (if known).



Fig. 2. The distribution of the hedgehog according to the 1979 enquiry. Open circles denote the number of negative answers (absence) and dots the number of positive answers (presence). The broken lines show the borders of the main regions of Sweden and the shadowed area shows the mountain and mountain-birch forest zones (Lindquist 1966). The predicted northern distribution limit is shown with the 150-day isocline (solid line).

along the coast in Norrland up to the province of Västerbotten (Fig. 1, Ekman 1922). Ekman mentioned that man had introduced hedgehogs into several places in Norrland. He also

questioned the spontaneous occurrence of hedgehogs as far north as the province of Upland (Fig. 1). The presence of hedgehogs in Hälsingland is said to originate from animals introduced in the late nineteenth century (Brehm & Ekman 1938, Notini & Haglund 1957).

3.2. Present distribution

The distribution of hedgehogs as indicated by the reports received is presented in Fig. 2. Hedgehogs are found in the south of Sweden (Götaland) and most parts of the central region (Svealand). In Norrland, they are found mainly along the coast up to the Finnish border.

The proportion of answers reporting the presence of hedgehogs was taken as an index of the numerical status of the hedgehog in different regions. This figure was higher for Götaland than for Svealand (Tab. 1) whereas the difference between Svealand and Norrland was not statistically significant. From the island of Gotland in the Baltic all answers but one reported the presence of hedgehogs.

The reports on changes in abundance during the last five years are unclear (Tab. 1). In each region, the answers are about equally distributed between the different categories. The proportion of answers reporting an increase was about the same in Götaland (24 %) and Svealand (28 %), but considerably lower in Norrland (14 %). The proportion indicating a decrease is lower in Götaland (22 %) than in the rest of the country (34 % — 29 %). The reports from the island of Gotland indicated a decrease in 53 % and an increase in only 4 % of the answers. In all regions, the proportion indicating no change constitutes a considerable part of the answers, which makes it difficult to interpret the results. The picture becomes clearer if one only looks at the relation between the "decrease" figures and the "increase plus no change" figures. In Götaland 70 % of the answers showed "increase plus no change" whereas only 30 % of the answers indicated "decrease". In Svealand and Norrland the reports showed about 55 % "increase plus no change" and about 45 % "decrease".

4. Discussion

It is only possible to obtain an approximate picture of the range expansion in Sweden because of the lack of previous investigations on the occurrence of the hedgehog. However, the data

Table 1. Distribution and estimated abundance of the hedgehog in the four main regions of Sweden. Numbers and percentages of replies.

	Gotaland		Gotland		Svealand		Norrland	
	Repl.	%	Repl.	%	Repl.	%	Repl.	%
Distribution								
presence	399	91	147	99	150	75	75	73
absence	39	9	1	1	50	25	28	27
total	438	100	148	100	200	100	103	100
Abundance								
increase	95	24	6	4	36	28	15	14
decrease	87	22	77	53	44	34	30	29
no change	110	28	50	34	15	12	22	21
no opinion	104	26	13	9	34	26	38	36
total	396	100	146	100	129	100	105	100

obtained strongly indicate that the hedgehog has expanded its range during this century. This is obviously primarily a result of intentional introduction (Fig. 1). The range expansion has occurred mainly along the coast up to the Finnish border. Kristofferson et al. (1966) showed that the hedgehog has been introduced many times into Finland, and this might have led to new local populations. Hedgehogs were even imported from Estonia and Russia in the beginning of the century. In Norway, the occurrence of hedgehogs has varied greatly over the years (Föyn & Huus 1947), but no detailed investigation has been performed. As in both Finland and Sweden, the occurrence of hedgehogs in certain places must have been a result of intentional introduction (Föyn & Huus 1947). Thus, in Finland, Norway and Sweden it is quite evident that man has influenced the occurrence of hedgehogs. In Finland, investigations by the Riistantutkimuslaitos (Kristofferson et al. 1966, 1977) show that the hedgehog expanded its range from 1952 to 1975 (Fig. 1). Furthermore, a considerable increase in the occurrence of hedgehogs was reported. The observed range expansion in Finland has obviously occurred much faster than in Sweden. One can only speculate about the reason for this. One reason could be the fact that the hedgehog has been introduced many times into Finland. Today, hedgehogs are found all over Finland except in the northern and north-eastern parts above the Gulf of Bothnia (Kristofferson et al. 1977). Roughly the same distribution pattern is seen in Sweden.

The north-western part of Sweden adjacent to Norway consists mainly of mountain and mountain-birch forest regions, which are unsuitable habitats for hedgehogs. The western limit of the hedgehog distribution cannot be stated with any certainty as there are too few answers

from the region between the coast in Norrland, where the hedgehog is found, and the mountain-birch forest zone.

It is reasonable to assume that the hedgehog, which hibernates in winter, needs a certain minimum length of time during the year to reproduce, to store energy for hibernation and for the young to grow enough to survive the first winter. I have calculated a "minimum time-span" to predict in which areas the hedgehog is expected to be able to establish a self-maintained population. The mating period is calculated to 30 days (Deanesly 1934), the gestation period to 32 days, and the weaning period to 38 days (Ranson 1941). The weaning weight is reported to be between 125 g and 345 g (Morris 1967). To survive the winter, the autumn body weight of a juvenile hedgehog must be about 700 g (Jungbluth 1978). Using a growth curve for juvenile hedgehogs with 250 g as the starting weight, I have estimated that it takes about 55 days to achieve a weight of 700 g (Kristiansson unpubl.). Addition of these minimum periods gives a "minimum time-span" of 155 days for the production of young. Furthermore, it is necessary for the adult, as well as the young, to have been able to store enough energy during this minimum time to cover their needs during the c. 200 day hibernation period. The length of the vegetation period, calculated as the number of days with a temperature of 3°C or higher (Ångström 1953), can be used as a measurement of invertebrate production (the main food of the hedgehog). The hedgehog is expected to be found south of the 150-day isocline and below the mountain-birch forest zone (Fig. 2). In fact, this seems to correspond rather well with the northern distribution limit of the hedgehog. However, answers reporting the absence of hedgehogs from the vicinity of the isocline are few and further reports

are needed. Of course, other constraints can affect hedgehog distribution: e.g., the availability of favourable winter nests, local climatic conditions and regularity in the arrival of spring and autumn.

The number of reports obtained from different provinces was too small to be used for a detailed analysis of changes in hedgehog numbers. The reports indicated that no general large-scale change in abundance occurred during the 5-year period until 1979. However, some changes might

have occurred locally. The status of the hedgehog is probably better in Götaland than in the rest of the country.

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Paper. II

**Demography and population dynamics of
a hedgehog population in Sweden**

ABSTRACT

A hedgehog population in southern Sweden was studied by capture-recapture during seven years (1972-1979). Each animal was weighed, sexed and marked with a numbered clip in each ear. The number of subadult and adult hedgehogs was about twenty in the first two years. Numbers then increased and approximately doubled when the population peaked. A decrease came the following year. The estimated number of juveniles produced varied between the years with the lowest figure in 1974 with a low population size (15 juv.) and the highest in 1977 (39 juv.) when the population size was large. No captured subadult female had suckled young, so the adult females were regarded as the reproducing part of the population. The average number of juveniles per adult female was 2.8. Recruitment rate did not show any correlation with subadult/adult population densities. For both juveniles and subadults the annual mortality varied greatly between the years. Average mortality was 47 % for subadults/adults and 34 % for juveniles. Summer mortality averaged 15 %, ranging between 3 % and 22 %. Traffic kills were the predominant cause of death in the summer. Most mortality occurred during winter, ranging between 26 % and 43 % (average 33 %) and increased with increasing non-juvenile densities. There were no statistical differences in age specific survival rate between males and females and, generally, no differences between the age categories within each sex in survival rate. It is argued that the population size appears to be more influenced by environmental factors, such as food availability, winter nest sites and winter climate, than by density-dependent factors.

INTRODUCTION

Data on population parameters such as density, mortality, number of juveniles born and recruited are fundamental for understanding the ecology of a species. Such information is available for a variety of animals, but is largely lacking for the European hedgehog. Only a few studies treating various aspects of its biology have been carried out (Morris 1969, Brockie 1974, Parkes 1975). The aim of this paper is to present data on demography and population dynamics of a hedgehog population in Sweden.

STUDY AREA

The study was carried out in a small village (Revingeby) in Scania, southern Sweden. The village covers about 50 hectares and is surrounded by abandoned arable land. The houses have gardens with lawns and there are usually bushes along the boundaries between the gardens. The village also contains four small groves with coniferous and deciduous trees and three large public lawns. Part of the village is abandoned arable land.

METHODS

In southern Sweden, hedgehogs become active after hibernation late in April or early May and the activity ends in September or October. Trapping efforts were made during this period, and, through the years (1972-1979) more than every third night was exclusively devoted to trapping. Trapping started at sun-set and ended at sun-rise. The hedgehogs were caught by hand with the aid of a powerful torch. Each animal was sexed, weighed and marked with a numbered clip in each ear.

The hedgehogs were classified as juveniles from birth to the first hibernation, and as subadults during the next summer until the second hibernation. Animals living in their third summer or more were called adults.

Juveniles were captured in August and readily distinguishable from subadult and adult animals. Subadults could only be distinguished from older animals during the first half of the season. However, unmarked animals captured in early spring could usually be separated into subadult/adult animals on the basis of size and weight in comparison with marked animals of known age, and, on the basis of general appearance, e.g. spine development. Later in the season this separation was not possible.

In the latter part of the study when nearly all of the animals (except juveniles in the autumn) were aged, unmarked animals captured in the spring

were in most cases subadults. Unmarked animals captured late in the season were categorized as subadults, if there were no indications that they were older.

RESULTS

Population size

In all years, the number of subadult and adult animals captured each season was similar to the number calculated with the Jolly-Seber method (Tanner 1978) (Tab. 1). This indicates that almost all subadult and adult individuals in the study area were caught.

The number of subadult and adult hedgehogs was about twenty in the first two years of the study. Numbers then increased and were doubled when the population peaked in 1978 (Tab. 1). A decrease came the following year. The yearly growth varied between the years with the highest rate in 1975-1976 ($r = 0.6$)

TABLE 1

Hedgehog population size and summer and winter mortality in the investigated population, 1972-1979. The Jolly-Seber method (Tanner 1978) was used to calculate the number of subadult/adult animals. The juvenile estimate was based on the number of juveniles captured and marked each year, the number of these marked juveniles recaptured in their second summer, and the number of unmarked subadults. A minimum number of unmarked animals were then estimated and added to the number of marked individuals (Boag and Murie 1981). The figures in parenthesis denote percentages.

Year	Estimated No. of animals (males and females)	No. of animals captured	Summer mortality. No. of animals found dead during summer caused by:		Winter mortality. No. of animals not recaptured the year after	Annual mortality. Total No. of dead during the year
			traffic	unknown		
1972 non juv	--	23	3(13)	0	6(26)	9(39)
juv	--	16	0	0	15(94)	15(94)
1973 non juv	23 $\pm$ 2.3	23	3(13)	0	6(26)	9(39)
juv	22	14	0	0	3(21)	3(21)
1974 non juv	21 $\pm$ 2.2	23	5(22)	0	1(4)	6(26)
juv	15	6	0	0	2(33)	2(33)
1975 non juv	34 $\pm$ 4.1	32	4(13)	0	12(30)	16(50)
juv	33	18	1(6)	1(6)	1(6)	3(18)
1976 non juv	53 $\pm$ 1.3	51	5(10)	1(2)	22(43)	28(55)
juv	33	17	1(6)	0	4(24)	5(30)
1977 non juv	52 $\pm$ 4.9	48	5(19)	3(6)	15(31)	23(48)
juv	39	32	1(3)	0	5(16)	6(19)
1978 non juv	57 $\pm$ 2.2	53	3(6)	3(6)	21(40)	27(52)
juv	17	13	0	0	5(38)	5(38)
1979 non juv	43 $\pm$ 1.3	40	1(3)	0	--	--
juv	16	7	0	0	--	--

and the lowest in 1978-1979 ($r = -0.3$) (Fig. 1). Average exponential growth rate for 1973-1978, calculated from the logistic equation was 0.7 (Tab. 1; linear regression $\ln \frac{(K-N)}{N} = a - rt$; $\ln \frac{56-N}{56} = 1.4 - 0.7 t$; $r^2 = 0.86$, $df = 4$, $t = 5.1$).

Recruitment

The estimated number of juveniles produced varied between the years with the lowest figure in 1974 (15 juv.) and the highest in 1977 (39 juv.) (Tabs 1 and 2). The juvenile density increased with increased adult and subadult densities throughout the years 1973-1977. In 1978 the subadult and adult density remained high but the recruitment dropped to a number similar to that in 1972-1974 with about half the subadult and adult densities (Tabs 1 and 2). The average number of juveniles per female, including subadults, was 1.43 but for the adult females separately this figure was almost twice as high (Tab.2). Since no captured subadult female had suckled young (Kristiansson unpubl.), the adult females were regarded as the reproductive part of the population.

Recruitment rate (number of juveniles per adult female) did not show any correlation with subadult/adult population densities (Fig. 2). In 1977, for instance, with high subadult/adult density the recruitment rate was almost as high as in 1973 with less than half the 1977 density. However, in the year of peak density (1978) and in the subsequent year, recruitment rate was considerably lower than in years with low densities (1973-1975).

Mortality and survival

For both juveniles and subadults/adults the annual mortality varied greatly between years (Tab. 1). Average mortality was 47 % for subadults/adults and 34 % for juveniles. Summer mortality averaged 15 % and ranged between 3 % and 22 %. Traffic kills were the predominant cause of death in the summer (Tab.1). The presented figures are minimum numbers. Part of the category "unknown causes" might have been traffic accidents, where the animal was not killed instantly. The percentage of the population killed by traffic was approximately the same through the years (except for 1974) with a tendency to a slight decrease in the latter part of the study. Except for a few instances, the animals killed by cars were adults and subadults (Tab. 1).

Winter mortality was measured as the number of animals not recaptured subsequent years. In general, most of the mortality occurred during the winter. For nonjuveniles, winter mortality ranged from 26 % to 43 % (average 33 %) and increased with increasing nonjuvenile density (Sperman rank; $r_s = 0.93$, $p = 0.01$, $N = 7$) (Fig. 3c). For subadults, winter mortality could only be calculated for the years 1975 to 1978. In both male and female subadults winter losses tended to increase with subadult/adult population density (Fig. 3a) and for subadult males the correlation was significant. The winter mortality of

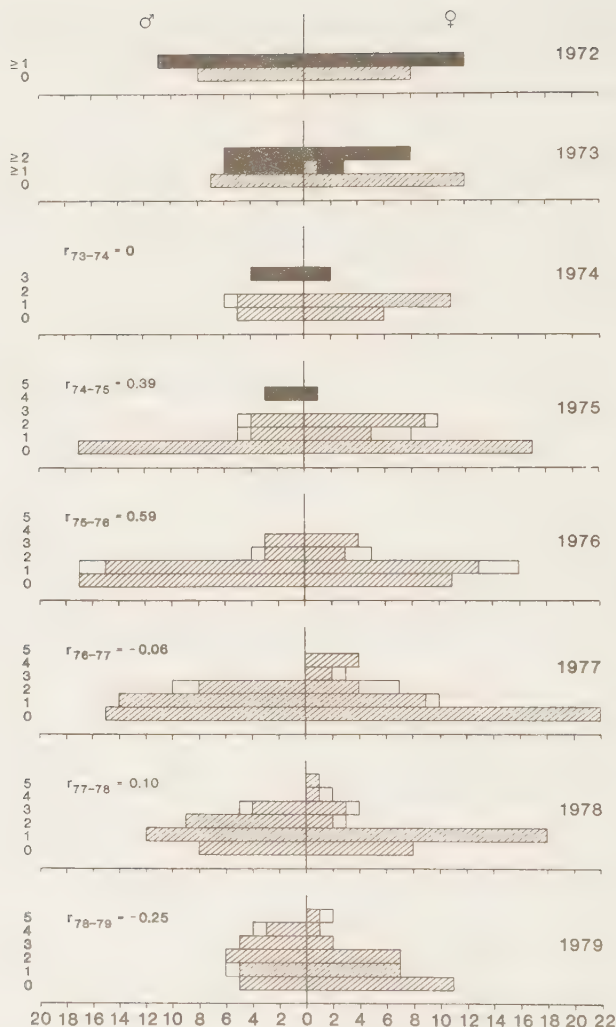


Fig. 1. Age distribution of the hedgehog population in 1972 through 1979. The material from 1972 contains only animals trapped in the autumn. The figures also include animals not being captured in one given season but on a subsequent occasion. Individuals captured late in the season were regarded as a part of the population from the beginning of that season. Open parts of the bars denote individuals not being age determined exactly. These individuals were placed in the nearest lower age category, usually age category 1 or 2. The presented number of juveniles was the minimum number of animals known to be alive. Growth rate, r_1 , was calculated from $r_1' = e^r - 1$, where

$$r_1 \text{ is } \frac{N_1 - N_0}{N_0} \text{ (Tanner 1978).}$$

Population size (N_0 and N_1) is the number in the population prior to reproduction (Tanner 1978).

TABLE 2

Estimated density of juvenile hedgehogs (size of study area was 50 ha) and the average number of juveniles recruited per female. Estimated number of juveniles are given in parenthesis. The number of females was the number known to have been alive at least to the 15th August.

Year	Density (no/ha)		Total	males/100 females		Recruitment	
	male	female				Juveniles/ subadult and adult females	Juveniles/ adult female
1972	0.16(8)	0.16(8)	0.32(16)	100	ns	1.33	-
1973	0.20(10)	0.24(12)	0.44(22)	83	ns	2.44	3.14
1974	0.16(8)	0.14(7)	0.30(15)	114	ns	1.36	(15)
1975	0.36(18)	0.30(15)	0.66(33)	120	ns	1.94	3.67
1976	0.38(19)	0.28(14)	0.66(33)	136	ns	1.27	4.13
1977	0.34(17)	0.44(22)	0.78(39)	77	ns	1.63	2.79
1978	0.18(9)	0.16(8)	0.34(17)	113	ns	0.61	1.70
1979	0.10(5)	0.22(11)	0.32(16)	45	ns	0.84	1.33
Average	0.24(94)	0.24(97)	0.48(191)	100	ns	1.43	2.79

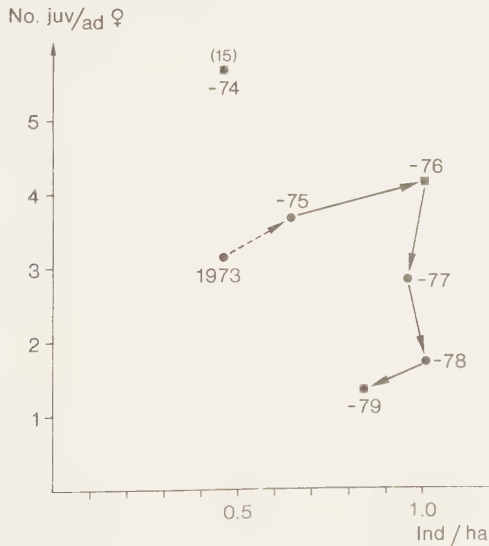


Fig. 2. Estimated recruitment rate calculated as the estimated number of juveniles per adult female, in relation to the density of subadult/adult hedgehogs.

% winter losses

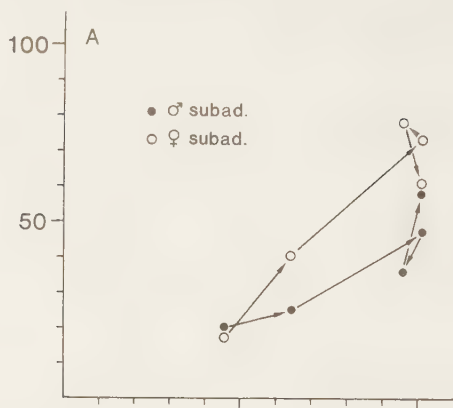
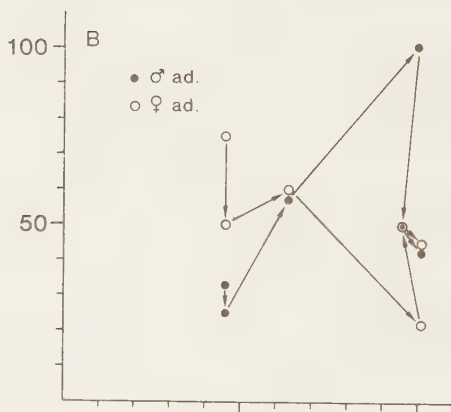
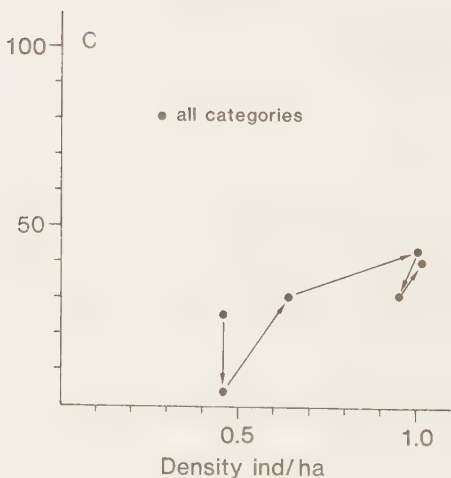


Fig. 3. Winter losses in relation to subadult/adult densities.

(a) for subadult males (filled circles) and subadult females (open circles), 1975 to 1979. (Sperman rank; males $r_s = 1.0$, $p = 0.01$, $N = 5$; females, $r_s = 0.60$, $p > 0.05$, $N = 5$).



(b) for adult males (filled circles) and adult females (open circles), 1973 to 1979. (Sperman rank; males, $r_s = 0.54$, $p > 0.05$, $N = 6$; females, $r_s = -0.779$, $p > 0.05$, $N = 6$). (c) for all categories, 1973 to 1979 (Sperman rank; $r_s = 0.93$, $p = 0.01$, $N = 7$).



(c) for all categories, 1973 to 1979 (Sperman rank; $r_s = 0.93$, $p = 0.01$, $N = 7$).

adult males and females showed no correlation with subadult/adult densities (Fig. 3b). Juvenile winter mortality varied greatly (ranging between 6 % to 94 %) and was not correlated with subadult/adult densities (Sperman rank; $r_s = 0.07$, $N = 7$, $p > 0.05$).

In the study area, December to February were the coldest months. Winter mortality among subadult and adult hedgehogs was correlated with the average deviation from normal temperature in the coldest months, i.e., a large negative deviation from normal temperature was associated with high winter mortality (Sperman rank; $r_s = -0.955$, $N = 7$, $p = 0.01$). Subadult/adult winter mortality was also positively correlated with the number of days with minimum temperature equal to or below 0°C (Sperman rank; $r_s = 0.955$, $N = 7$, $p = 0.01$). But juvenile winter mortality was not correlated with these environmental factors (Sperman rank; average temperature deviation from normal temperature December to February, $r_s = 0.143$, $N = 7$, $p > 0.05$; number of days $\leq 0^{\circ}\text{C}$, $r_s = 0$, $N = 7$, $p > 0.05$).

Body weight in autumn was taken as an index of the amount of fat stored, which influences winter survival. Because of different latest capture date, autumn body weight was recalculated from growth curves (Paper VI) to weight at October 15th for different categories. Juveniles and subadult males that survived winter were heavier than nonsurviving animals (juveniles; t-test, $t = 2.24$, $p = 0.013$, $df = 110$; subadult males, t-test $t = 3.27$, $p = 0.002$, $df = 30$). But for adult animals and subadult females no relationship between autumn body weight and winter survival was found (t-test, all cases $p > 0.3$).

Except for a tendency for juvenile females to survive better than juvenile males ($\chi^2 = 3.03$, $0.05 < p < 0.1$, $df = 1$) there was no statistical difference in age specific survival rate between males and females (χ^2 -test and Fisher exact, $p > 0.1$, $df = 1$, all cases) (Tab. 3). In males, there was no difference in survival rates of different age categories (χ^2 -test and Fischer exact, all cases $p > 0.1$). Data showed a higher survival of juvenile females when compared with subadult females (category 1; $\chi^2 = 7.5$, $0.001 < p < 0.0$, $df = 1$) but juveniles did not show higher survival when compared with age category 2 ($\chi^2 = 0.13$, $p > 0.1$, $df = 1$). There was no difference between the other female-categories (χ^2 -test and Fisher exact, all cases $p > 0.1$).

The combined male and female age specific survival rates showed no difference between the categories, although the juvenile category had a tendency to survive better than the rest (juveniles, $\chi^2 = 3.69$, $0.05 < p < 0.1$, $df = 1$, all other cases $p > 0.1$). Average further life expectancy for juvenile males was 1.6 years and for females 1.8 years. However, further life expectancy calculated from the estimated survivorship was 1.2 years for males and 1.3 years for females.

TABLE 3

Survivorship tables based on trapping data from 1973-1979. Age specific survival rate was estimated by combining data from different cohorts. An estimated survivorship table was calculated (l_x). The starting point was the estimated litter size at birth, obtained by calculating backwards from the average observed litter size (5.2 at the age of 3-6 weeks, Kristiansson 1981a) and using a mortality estimate of 0.2 from birth to weaning (Morris 1977). Apart from age category 0 and 1 given a litter size of zero, the calculated litter size was set at 6.5. Juvenile survival rate was 0.4 for females and 0.32 for males.

Category (month)	age-specific survival rate		survivor l_x		Estimated No. of survivor l_x	
	males	females	males	females	males	females
0 (1-3)	0.56	0.69	1.00	1.00	1.00	1.00
1 (9-14)	0.58	0.43	0.56	0.69	0.32	0.40
2 (21-26)	0.50	0.61	0.32	0.30	0.19	0.17
3 (33-38)	0.43	0.67	0.16	0.18	0.10	0.10
4 (45-50)	0	0.40	0.07	0.12	0.04	0.07
5 (57-62)	0	0	0	0.05	0	0.03
6 (69-74)	0	0	0	0	0	0

Age and sex structure

The age distribution changed through the study period (Fig. 1). From 1972 to 1974, the age structure was that of a decreasing or a stable population, which in 1975 to 1977 changed into one of increasing numbers and again in 1978 and 1979 into an aging population.

Sex ratio among subadult and adult animals was equal as was the sex ratio in each age category and year (1978, $\chi^2 = 3.0$, $0.05 < p < 0.1$, $df = 1$, all other cases $p > 0.1$, $df = 1$). Also the juvenile sex ratio was equal (χ^2 -test, all cases $p > 0.1$).

DISCUSSION

Reproduction

In Sweden female hedgehogs do not produce young until during their third summer when being about two years old (this paper, Löfqvist pers. com.). In Britain, oestrus is setting in when the female hedgehog reaches adult body weight which is in the second summer (Deanesly 1934). In my study area, subadult females reach average adult body weight in August during their second summer

(Paper VI), but no mating behaviour was observed at this time (Paper V). Edwards (1957) stated that, if not well fed, captive hedgehogs may not breed until the beginning of their third summer.

In England, some female hedgehogs may breed twice in one season (Deanesly 1934, Morris 1969). There is no indication of a second litter in Sweden (Kristiansson 1981a and b).

Mean litter size in Sweden was reported to be 5.2 young at the age of three to six weeks, and, litter size at birth was calculated to be 6.5 (Tab. 3, Kristiansson 1981a). In the study area, the average estimated number of juveniles per adult female in autumn was 2.79. The discrepancy between estimated litter size at birth and the recruited number of juveniles per adult female suggests a high mortality rate from birth to weaning (Tabs 2 and 3). Morris (1969) estimated survival for juveniles over their first winter to be around 35 %, he believed that this may still be a conservatory figure, as it did not take into account animals which died during the summer month after weaning. The figures correspond well with the estimated survival rate shown in Tab. 3.

Survival and mortality

The discrepancy between the age-specific survival rate calculated from capture data and the estimated age-specific survival rate based on the estimated litter size at birth (Tab. 3) may be due to animals dying before weaning and never being captured. My results indicate a more or less constant survival rate among the different age categories. During the first year of life mortality rate of British and Swedish hedgehogs was approximately twice as high as that of New Zealand animals (Fig. 4). One explanation for this difference could be the longer and harsher winter in Britain and Sweden (Brockie 1974). Among the older categories, hedgehogs in Sweden tended to survive less well than those in Britain, while survival among New Zealand hedgehogs was markedly higher (Fig. 4).

Mortality occurred predominantly during winter (Tab. 1). Winter mortality was recorded from the start to the end of hibernation, as indicated by the first observed hibernating animal and the last recorded arousal. Some deaths recorded as winter mortality may have occurred during late autumn or early spring, so strict winter mortality may be somewhat less. Since mortality was estimated from trapping data, the cause of death is unknown. Important might be lack of energy stored as fat, as the amount of fat stored is essential for survival during hibernation, and hedgehogs experience substantial weight loss during winter (Paper VI, Kristoffersson and Suomalainen 1964, Brockie 1974). This will probably be critical, especially for juveniles. My data showed for juveniles and subadult males a correlation between the autumn body weight and the survival. The absence of correlation in other groups may be due to the

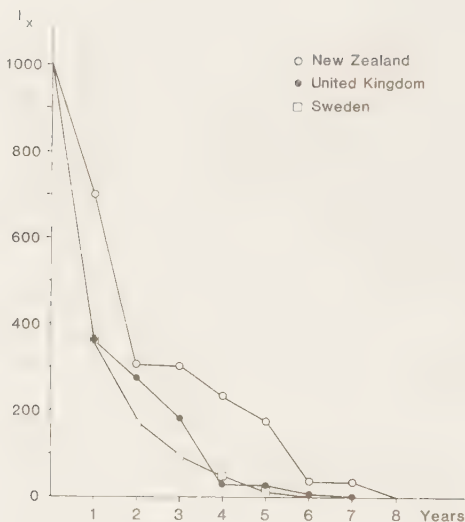


Fig. 4. Survivorship curves (males and females combined) of New Zealand, British and Swedish hedgehogs (Morris 1969, Brockie 1974).

difficulty of trapping the animals close to the start of hibernation. Also body weight as an index of fat amount might not be appropriate. Although Brockie (1974) found a relation between body weight and fat index, he states that "small" hedgehogs may carry large deposits of fat or may lack fat altogether.

Environmental factors could be expected to influence winter mortality, but only subadult/adult winter mortality was correlated with temperature. For juveniles other factors, such as the winter nest quality and the ability to build winter nests, may be more important. Morris (1973) found that most hedgehogs that died in their nests during winter were juveniles, probably too inexperienced to construct an adequate protective nest.

A clear increase of winter mortality with increasing densities was evident for the subadult categories (3a and b). It might be that social dominance has an influence on the acquisition of the hibernation sites and that subadults, due to their probably subordinate status, are the first animals to suffer from increasing densities. One could argue that the recorded density-dependent winter mortality in subadults is a result of emigration from the study area, as emigration can not be separated from actual winter mortality with this method. Göransson et al. (1978) investigated road mortality of hedgehogs, including the study area and covering a distance of 17 km away from that area. They never found any marked hedgehogs killed outside the study area. Also the hedgehog populations in villages around the study area at distances between 5 and 10 km were extensively studied by capture-recapture, but no hedgehogs from the study area were recorded. Only one occasion of emigration has been observed, i.e. one juvenile female appearing in a village (Vomb) at a distance of 6 km

from her birth place (Kristiansson unpubl.). If this animal had moved there by itself or been transported there by humans is unknown. Further, radio tracked adult hedgehogs did not leave the study area. Thus all available information indicates that most of the winter disappearance is actually winter mortality. Road kills have been regarded as a threat to the hedgehog population in Sweden. Generally, this concern is exaggerated (Göransson et al. 1978, Tab.1). In some cases, e.g. populations with a small number of reproducing adult females, road killing of a few females may curtail population growth. Due to the large movement activity during the mating period, male hedgehogs were mainly killed during this period. Females were mainly killed during the post-mating period, probably due to the increased activity after the weaning of the young (Göransson et al. 1976, Paper V).

Population regulation

What factors regulate or limit numbers of the examined hedgehog population? The relationship between density and recruitment might suggest a delayed density-dependent relation (Tab. 2, Fig. 2). The fact that females do not normally breed until they are 2 years old may promote delayed effects on the population. However, although the study covers six years the study period is too short to give a definite answer. Summer mortality was about constant and showed no density-dependence through the years (Tab. 1). Of the different categories only subadults showed increased winter mortality with density (Fig. 3). Thus, the population showed only some features of density-dependent regulation.

Weather and the length of the summer season probably plays an important part in regulating the population, as is indicated by studies in England and New Zealand. In New Zealand, the summer is long and mild, which enables the females to have two or three litters per year (Brockie 1957). In Britain, the summer is shorter and harsher, and only some females have two litters per year (Brockie 1957, Morris 1969). The summer and breeding season is shortest in Sweden, and no second litters are known (Kristiansson 1981a and b). Inclement weather during autumn could affect the possibilities for hedgehogs to obtain enough food to store as fat, and cold and dry weather in spring may affect the survival of animals which are in bad condition after the hibernation. Winter temperature lower than normal means higher winter mortality, which in turn may be due to the differential quality of winter nests, and it is possible that this and the availability of winter nest sites plays an important part in limiting the number of animals in the population (Morris 1969). Food availability is a factor that is always found in the background. High food abundance might mean higher survival rate, because it is easier to collect adequate amount of food in preparation for the winter. It might also mean that it is

easier to recover in the spring after a hard winter. No evidence of substantial predation or disease has been found in Sweden and Britain, and, it is unlikely that either predation or diseases regularly limit population growth of hedgehogs (Morris 1969). The population appears to be more influenced by environmental factors than by density-dependent factors, which, however, to some extent influence population growth.

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Paper III

Young production of European hedgehog
in Sweden and Britain

Young Production of European Hedgehog in Sweden and Britain

ROZRODCZOŚĆ JEŻY W SZWECJI I WIELKIEJ BRYTANII

Hans KRISTIANSSON

Kristiansson H. 1981: Young production of European hedgehog in Sweden and Britain. *Acta theriol.*, 26, 34: 504—507 [With 2 figs.].

Mean litter size in Sweden was calculated from enquiries and found to be 5.2 young per female and year. Comparable results from Britain have given 3.7; including second litters yield an annual young production of 4.8. A theory on the geographic variation in litter size proposed by Spencer & Steinhoff in 1968 was tested and was partially supported.

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INTRODUCTION

The European hedgehog (*Erimaceus europaeus* Linnaeus, 1758) is a common species in urban and suburban areas in most parts of Europe. In spite of this, little information is available on demography of hedgehog populations. Some information is, however, available on litter size (B. Morris, 1967; P. A. Morris, 1977). In this paper I present data on litter size of the hedgehog in Sweden. I will also test a theory proposed by Spencer & Steinhoff (1968) They suggested that the shorter seasons of more northern latitudes or higher altitudes, limit the number of times an animal resident in those areas is able to reproduce in its lifetime compared to its relatives in more southern or lower regions. It should therefore become advantageous for an animal to invest its energy in a few, large, early litters even when doing so reduces both its life expectancy and the total reproductive contribution to a level below the maximum achievable by many small litters.

METHODS

The data used were obtained in two ways: from enquiries on the distribution and abundance of the hedgehog in Sweden and by personal communications.

The young hedgehogs leave the nest at an age of three to four weeks, but remain together before being weaned, usually within 38—44 days of birth (Ranson, 1941). The records used in this paper refer to observations of young when leaving the nest up to weaning, i.e., young at an age of three to six weeks.

RESULTS

Reports on eighty-five litters were obtained from all over Sweden. The mean litter size was 5.2 ± 2.0 (0.2) (mean $\pm$ SD, SE). There was no statistical difference between the different regions in Sweden. However,

there was a tendency to larger mean litter size in the middle and northern regions of Sweden. The most observed litter size was five (27%) and litter sizes ranged from one to eleven (Fig. 1). Litter sizes from three to seven (3, 4, 5, 6) constituted 72% of the reports.

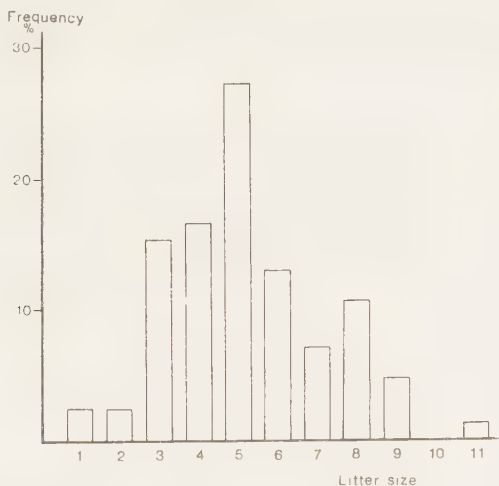


Fig. 1. The distribution of observed litter sizes in Sweden. Mean litter size was 5.2, $SD=2.0$ and $N=85$.

DISCUSSION

The figures obtained on litter size in Sweden can be compared with corresponding data from Britain obtained in the same way (Morris, 1977). The mean size of litters at an age of three to six weeks was 3.7 (Fig. 2). The value differs from that in Sweden ($p<0.001$, $df=126$, two-tailed Student's t -test). Not only is mean litter size larger in Sweden but also the observed range of litter sizes (Fig. 1 and Fig. 2). Some observations from England (Deanesly, 1934; Morris, 1969) indicate, that female hedgehogs can produce two litters per year, but it is not known how often this occurs. In Sweden, second litters are unknown and due to the short season, it is hardly possible for a female to produce a second litter. A rough estimate of the "maximum" extent of second litters in England can be obtained from Deanesly's data (1934): from morphological results some 29% (nine out of 31) of the females that have had one litter had the potential of producing a second litter. If we assume that the first and the second litter are

affected to the same degree by mortality (20% of the prenatal litter size up to the age of one month—Morris, 1977), and that both have the same prenatal litter size, then, the annual juvenile production per female would amount to 4.8. This estimate indicates a lower annual production per female in Britain than in Sweden.

Spencer & Steinhoff's (1968) theory may be applied in a comparison between Sweden and Britain. One would expect that the harsher climate

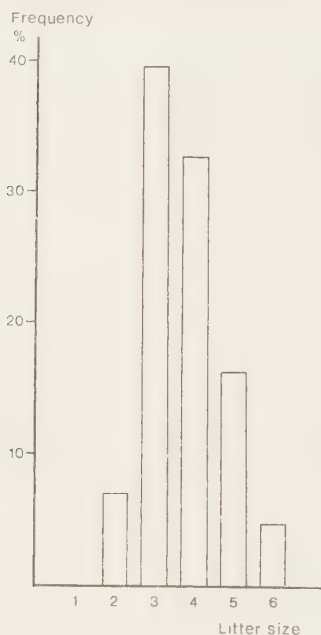


Fig. 2. The distribution of observed litter sizes in England (Morris, 1977). The categories "late young" and "seen" are pooled and correspond to the Swedish reports. Mean litter size was 3.2, SD=1.0 and N=43.

of Sweden restricted the breeding season. The length of the main breeding season is about four months in England (Morris, 1969), and about two months in Scania; South Sweden (Kristiansson, pers. obs.). The shorter breeding season in Sweden limits the number of times a female can reproduce in a given season and in a lifetime, and thus phenotypes which produce a few, large litters should be favoured. In Britain, with the longer breeding season, phenotypes which produce many and smaller litters would be favoured. The data presented here agree with these predictions. One consequence of the theory is that

the life expectancy should be shorter in Sweden than in Britain. Morris (1969) calculated life expectancy at weaning for a hedgehog population in England to be 1.9 years. Using capture-recapture data from a population in Scania I have found the corresponding value to be slightly more than two years i.e. almost the same (Kristiansson, unpubl.), which does not agree with the predictions made by Spencer & Steinhoff (1968).

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Paper IV

Home range size of the European hedgehog
(*Erinaceus europaeus*) in South Sweden

ABSTRACT

Home range sizes of hedgehogs in South Sweden were determined by hand captures and by radio-tracking. Home range boundaries were drawn according to the convex polygone method. The number of captures and the number of radio-tracking nights highly influenced the estimated size of the home ranges. Estimates based on less than 14 captures were significantly lower than estimates based on a higher number of captures. Therefore only estimates based on > 14 captures were used when comparing ranges of different categories. Significant differences were found between males and females and between subadults and adults. Home range estimates for adult individuals obtained by radio-tracking were about three times larger (males: 46.5 ha; females: 19.7 ha) than those obtained by hand captures (males: 12.9 ha; females: 6.7 ha). For subadults, home range estimates obtained by hand captures were 30 - 50 % less than those obtained for adult individuals (males: 9.2 ha; females: 3.4 ha). Home range estimates based on hand captures were corrected for sample size biases. For adult individuals, the corrected home range estimates were about 30 % lower than those based on radio-tracking.

INTRODUCTION

Much time and effort have been spent in determining the area traversed by an animal during its normal daily activity, i.e. its home range (Burt 1943). Generally, home range size varies between individuals and in different environments; among other things food supply influences home range size as has been shown experimentally (Simon 1975, Mares et al. 1976). Reported variation in home range size can also be due to the method of estimating the range, or the number of captures used in calculating the home range size (Mares et al. 1980). On a theoretical basis, Jennrich and Turner (1969) tabulated correction factors for sample size biases.

The hedgehog is a nocturnal insectivorous mammal which spends the winter in hibernation. It is often found in connection with human settlements. In my study, home range has been examined in two ways, i.e. capturing the hedgehogs by hand and radio-tracking.

The purpose of this investigation is to study the relation between the number of captures and the observed size of the home range, and to compare estimates from capture with results based on radio-tracking. The size of home range will also be discussed in relation to sex and age of the hedgehogs.

STUDY AREA

The study was carried out in a small village, Revingeby, in southernmost Sweden. The village covers about 50 hectares. There are about 500 inhabitants and 200 houses. About one fourth of the houses are old with large gardens, most of which contain sheds and composts. There are four small groves in the village, three of which are deciduous and one coniferous. Three large lawns are important foraging places for the hedgehogs.

METHODS

Live trapping

During the years 1973-1978, hedgehogs were caught by hand at night with the aid of a powerful torch. The captured animals were sexed, weighed and marked with a numbered clip in each ear. The capture site was noted on a map and the animal was released at the place of capture. For each individual, all captures obtained during one season were plotted on a map and the boundaries of its home range were drawn according to the convex polygone method (Mohr and Stumpff 1966). Altogether, 155 home ranges were calculated and corrections for sample size biases were employed according to Jennrich and Turner (1966). Four

categories of animals were distinguished, i.e. subadult males, subadult females, adult males and adult females. Individuals were regarded as subadults in their second summer of life and as adults from the third summer. For each category, the estimated home range size from the different years were pooled and plotted against the number of captures. Five points moving averages were calculated for each category.

Radio tracking

For detailed information on movements and home range sizes individuals with known age were radio-tracked. The transmitter, a rectangular plate weighing about 20 grams, was cemented on the rear part of the back, where the spines had been cut down in a small area. A single portable receiver (frequency 27 MHz) with a loop antenna was used. The signals were obtained within a radius of 75 to 100 m. Five adult males and six adult females were radio-tracked, on each occasion during a whole night, roughly between 2000 and 0400 hrs. During the night, positions were taken at 30 minutes intervals. Each night of radio-tracking was considered as one observation when the cumulative convex polygon estimates were plotted against the number of radio-trackings. The eleven individuals were radio-tracked altogether in 114 nights.

RESULTS

Live trapping

When examining the effect of the number of captures on home range size, moving average curves were calculated. For each category, the part of the curve where it levels out was determined. For all categories, the curves raised between 5 and 14 captures before they started to level out (Fig. 1). Home range estimates based on 14 captures or more were significantly larger than estimates based on fewer captures (t-test, all cases $p < 0.05$, Tab. 1). Thus, when comparing home range size of different categories, estimates in the region of asymptotic approach (≥ 14 captures) were used.

Correction factors for sample size biases (Jennrich and Turner 1969) were used to remove the effect of biases depending on number of captures. Corrected home range estimates were calculated. Estimates based on 14 captures or more did not differ from estimates based on fewer captures (t-test, all comparisons, $p > 0.01$, Tab. 1). Thus, in this case all estimates were pooled. Corrected home range estimates were three to four times larger than those obtained from uncorrected data.

Significant differences in home range between the examined categories of hedgehogs appeared in both uncorrected and corrected estimates (Tab. 1). Home

TABLE 1

Mean home range size of different categories of hedgehogs during a year, determined by hand captures. Corrected home range sizes were calculated according to Jennrich and Turner (1969). Three categories of data were considered: (1) a low number of captures (< 15 and < 14 for males and females, respectively), (2) a high number of captures (> 15 and > 14 for males and females, respectively), (3) all captures included. The figures in parenthesis denote the number of hedgehogs. Only individuals captured more than 14 (females) and 15 (males) were included, when testing differences in uncorrected home range estimates. Mann-Whitney U-test (one way) was used.

adult males - adult females $U = 18$, $p < 0.05$
 adult males - subadult males $U = 41$, $p < 0.05$
 subadult males - subadult females $U = 4$, $p < 0.05$
 adult females - subadult females $U = 21$, $p < 0.05$

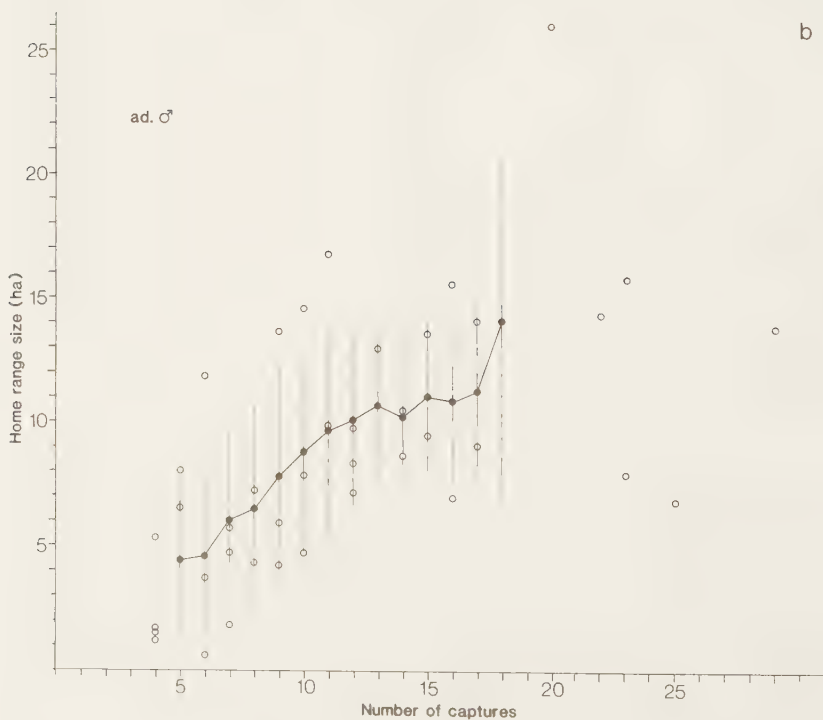
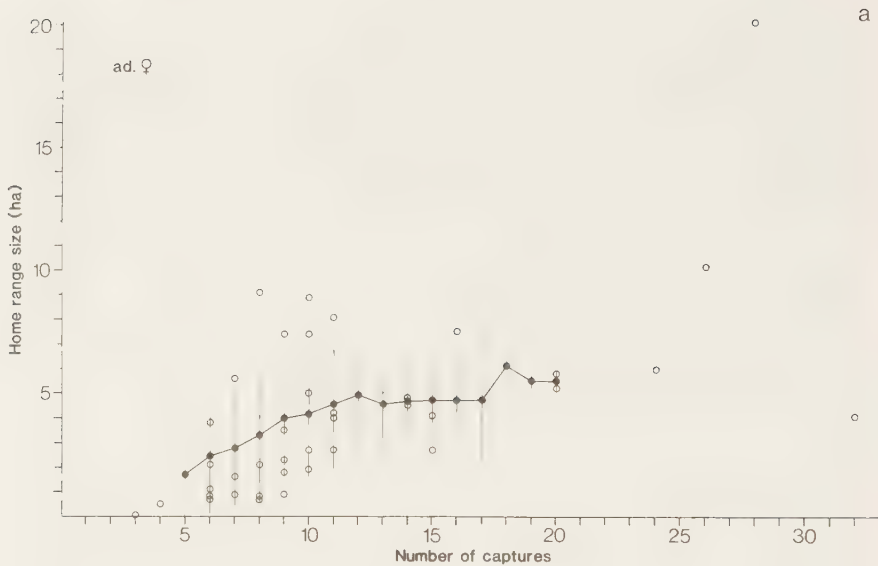
Corrected home ranges showed the same relation as uncorrected home ranges (t-test, all cases $p < 0.05$).

		Home range size (ha) $\bar{x} \pm$ SD: SE			
		adult		subadult	
		biased	corrected	biased	corrected
males, < 15		$7.4 \pm 4.1(0.8)$ (28)	$31.9 \pm 16.0(3.0)$ (28)	$5.4 \pm 4.2(0.9)$ (23)	$22.0 \pm 14.8(3.1)$ (23)
females, < 14		$3.2 \pm 2.7(0.5)$ (28)	$13.6 \pm 10.1(1.9)$ (28)	$1.4 \pm 0.8(0.2)$ (27)	$9.2 \pm 9.2(1.8)$ (27)
males, > 15		$12.9 \pm 5.2(1.4)$ (13)	$28.8 \pm 11.3(3.1)$ (13)	$9.2 \pm 4.6(1.3)$ (13)	$20.7 \pm 9.5(2.6)$ (13)
females, > 14		$6.7 \pm 4.6(1.3)$ (12)	$14.6 \pm 8.8(2.5)$ (12)	$3.4 \pm 1.5(0.4)$ (11)	$7.9 \pm 3.3(1.0)$ (11)
males, < 15 and > 15		$9.2 \pm 5.1(0.8)$ (41)	$30.9 \pm 14.6(2.3)$ (41)	$6.8 \pm 4.6(0.8)$ (36)	$21.5 \pm 13.0(2.2)$ (36)
females, < 14 and > 14		$4.3 \pm 3.7(0.6)$ (40)	$13.9 \pm 9.6(1.5)$ (40)	$2.0 \pm 1.4(0.2)$ (38)	$8.8 \pm 8.0(1.3)$ (38)

ranges of male hedgehogs were two to three times larger than those of the females. This concerns both biased and corrected figures.

Radio-tracking

For males, the calculated home range size increased rapidly with increasing number of radio-trackings (Fig. 2). This especially concerns males, which were tracked in May and early June, i.e., at the beginning of the hedgehogs' season of activity, which includes their main mating period (Paper V). Calculated home ranges of these males were considerably larger than those tracked later in the season. In females the increase of home range size with number of recordings was slower and the final estimates of their home range size were much lower; on average less than half the size of the ranges of adult males



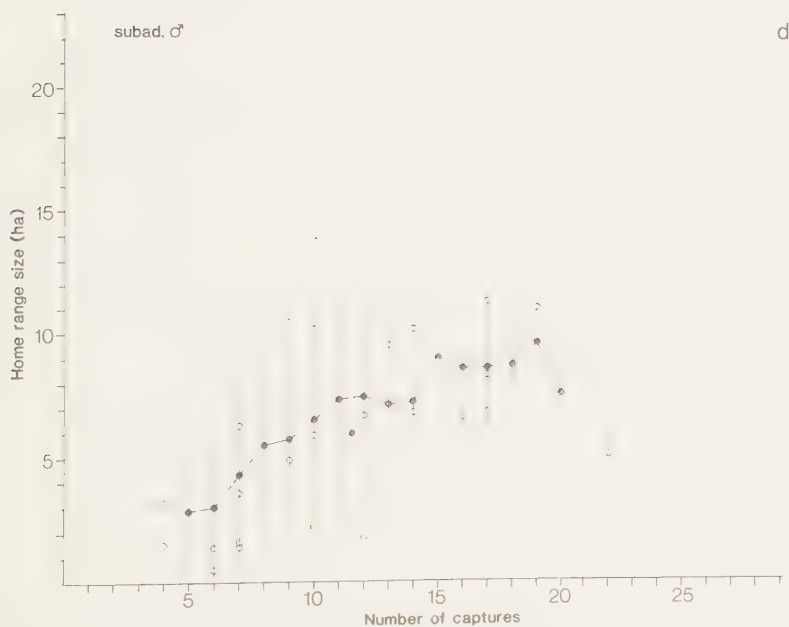
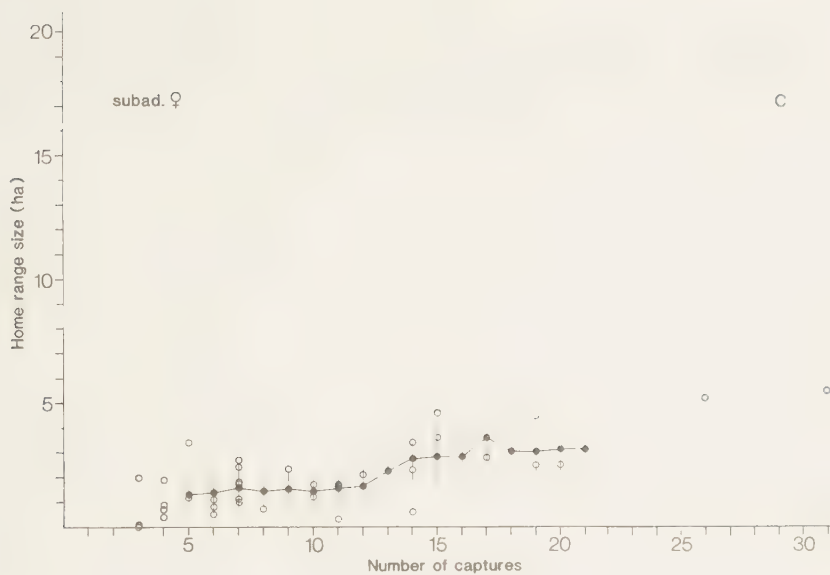


Fig. 1. (a-d) Yearly home range size of different categories of hedgehogs in relation to the number of captures (up to 18-20 captures). Home range was calculated according to the convex polygon method. For each category, the home range estimates from the years 1973 to 1978 have been pooled. The curve indicated by black circles is based on five points moving averages. Vertical lines show standard deviation.

(Tab. 2). Home range sizes obtained by radio-tracking were about three times larger than the figures obtained by hand captures not being corrected (Tabs 1 and 2). Also the corrected home range estimates were lower (about 30 %) than those based on radio-tracking (Tabs 1 and 2).

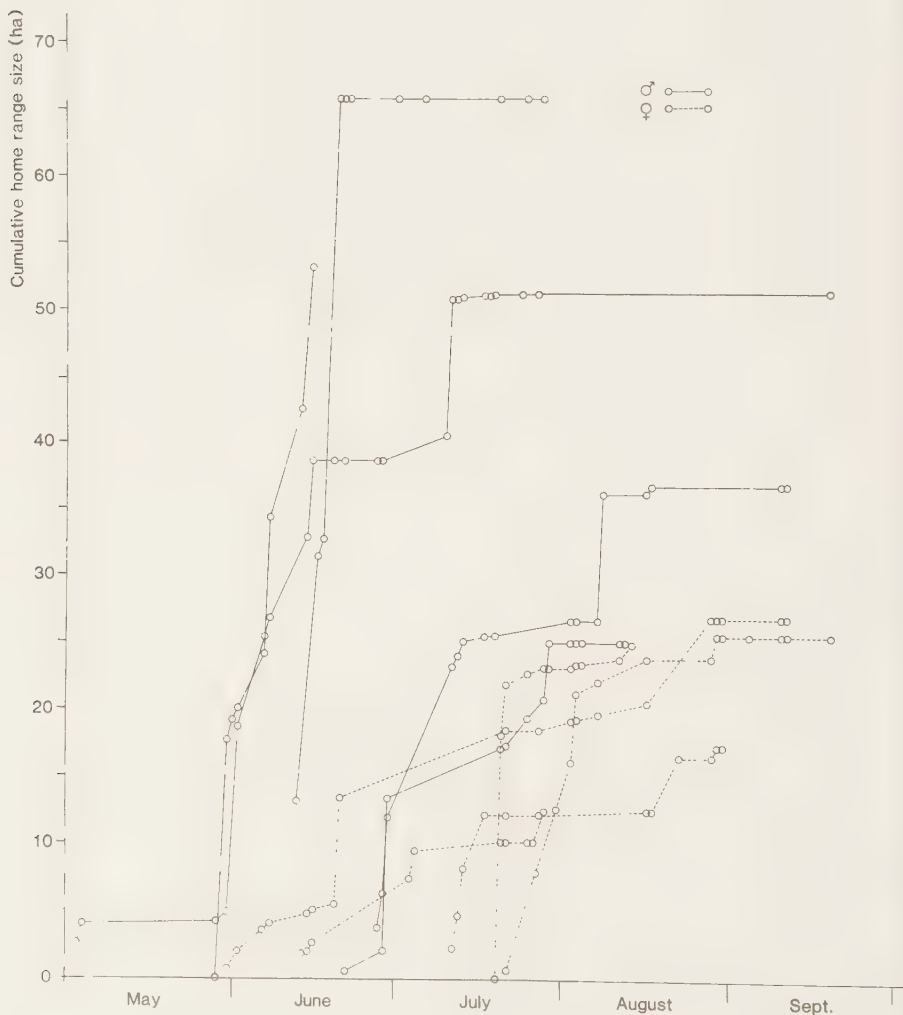


Fig. 2. Cumulative estimates of five males' and five females' home range sizes determined by radio-tracking. Each night of radio-tracking is shown by an open circle. All radio-tracked individuals were adults.

TABLE 2

Average home range size of adult males and adult females, determined by radio-tracking. Mann Whitney U-test (one way), $U = 2$, $p < 0.05$.

	$\bar{x} \pm SD$	range	sample size
Males	46.5 ± 15.8	25.0 - 65.7	5
Females	19.7 ± 8.4	8.1 - 29.5	6

DISCUSSION

The minimum number of captures needed for a reliable estimate of home range size by use of the live trapping method (without corrections) was at least 14 captures (Fig. 1). In adult individuals, home range estimates based on radio-tracking gave three to four times larger estimates than those of hand captures (Tabs 1 and 2). This shows that the curves levelling off as in Fig. 1 might result from the mechanics of trapping and is not in itself a proof of an accurate size of the home range (cf. Hayns 1949). The discrepancy may be due to one or more of the following factors: (1) live trapping success is much dependent on chance; (2) irregular use of home range and extensive movements lead to few captures in the peripheral parts of the animal home range; (3) radio-tracking gives possibilities of tracing animals in places where it is almost impossible to detect and capture animals; (4) rapid and extensive movements, e.g. among adult males in the mating period are difficult to record by hand captures but are obtainable by radio-tracking.

The presented uncorrected home range sizes of the different categories assume that the individuals had the central parts of their home ranges examined. By using correction factors, this problem estimation is bypassed. The correction factors tabulated by Jennrich and Turner (1969) compensated for differences in sample size, and this resulted in consistent estimates of home range size in spite of variations in the original data. The corrected estimates were approximately two-thirds of those obtained by radio-tracking (Tabs 1 and 2). The difference may be due to one or several assumptions in Jennrich and Turner's model not being fulfilled, e.g. random sampling of the animal throughout its whole range (point 2 above).

The coefficient of variation for home range size was large for all categories, spanning between 40 and 100 %. Thus, even when the influence of the number of captures is minimized, the individual variation is still left as an uncontrollable variable. A similar degree of individual variation in home range sizes has been found in free ranging domestic cats (Liberg 1984). In

Eastern chipmunks (*Tamias striatus*) the number of captures was found to have a predominant influence on the estimate of home range size (Mares et al. 1980). Neither age, sex, year nor any combination of these factors accounted for a significant amount of the observed variation; each combined accounted only for 1.3 % of the variation, and each of the factors for less than 1 %. Obtained data in this study confirm the importance of the number of captures on home range size estimate. However, the number of captures is seldom taken into account, which makes reported figures on home range sizes uncertain. Without any corrections, the minimum captures necessary for reaching asymptotic level in a recapture curve for hedgehogs was 14 or more. Corresponding figure for chipmunks was 20. As enough data on each animal is difficult to obtain (in this study data on only 44 estimates out of 155 could be used), the best choice when estimating home range size by hand captures is to apply the correction factors of Jennrich and Turner (1969). The second choice is to investigate the effect of number of captures on the estimate and choose those in the region of asymptotic approach.

Males were found to have significantly larger home ranges than females and adults had significantly larger home ranges than subadults (Tabs 1 and 2). This concerns both hand captures (corrected and uncorrected estimates) and radio-tracking data. The figures in this study are larger than previous reports on hedgehog home ranges. In New Zealand, the average size of the home range based on capture-recapture, was reported to be 3.6 ha for adult females and 2.5 ha for males in one study (Parkes 1975) and on the average 18 ha (range 5.1 - 25.9 ha, both sexes) in another study (Brockie 1974). From European Russia, Karaseva et al. (1979) reported home range sizes between 0.5 and 11.2 ha with a mean of 8 ha for males and 2.6 ha for females. In these studies, the number of captures is not reported and its influence on home range figures is unknown. Besides, subadults are not separated from adults. However, the latter figures are similar to the estimate with sample size not being corrected for (Tab. 1). Also in radio-tracking the estimates of home range size depend on the number of radio-fixes or tracking periods. The mean size of home range reported for adult males in England was 32 ha ($n = 6$) and for adult females 10 ha ($n = 7$) (Reeve 1982). Further, subadult home range estimate was 12 ha (sex not given, $n = 3$). The sizes are smaller than found in my study (adult males $\bar{x} = 46.5$ ha, adult females $\bar{x} = 19.7$ ha). The difference could partly be explained by differences in the number of fixes and tracking nights and partly by different environmental conditions such as in food availability.

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Paper V

Spatial organization and mating system
in a hedgehog population

ABSTRACT

Spatial organization of a hedgehog population in southern Sweden was studied using capture-recapture technique and radio-tracking. Home ranges of individual hedgehogs of the same and opposite sex greatly overlapped, indicating absence of spatial separation. The summer was divided into a mating period and a post-mating period, based on the distribution of observed mating attempts. Adult males made mating attempts with several females and individual adult females were courted by several males. During the mating period adult males showed high movement activity (June 52 m/15 min.) which decreased significantly during the post-mating period (August 29 m/15 min.). For adult females movement activity was less than for adult males during the mating period (June 23 m/15 min.). In the post-mating period adult males and females showed similar movement activity (females in August 27 m/15 min.). Throughout the summer the hedgehogs were continuously active during the nights. Generally, the level of aggression was low. The hedgehog did not show any territorial behaviour neither within nor outside the mating period. It is argued that the mating system of the hedgehog population is a case of overlapping promiscuity governed by the temporal and spatial distribution of food resources. The solitary habit gives the searching and strictly promiscuous behaviour an advantage over other alternatives.

INTRODUCTION

The variation in mating system among species is due in part to phylogeny (e.g. mammalian males are released from nursing the young as the males lack functional mammary glands) and in part to ecology (Brown 1975). Comparative studies on different groups of animals and species living in different habitats show that ecological factors are important in shaping mating systems, spatial behaviour and partitioning of parental care between males and females (Krebs and Davies 1978 and 1981, Wittenberger 1981). Further, male and female interests overlap, but they are never congruent (Wittenberger 1981).

The European hedgehog (*Erinaceus europaeus*) is a large-sized insectivore mainly with nocturnal and secretive habits. Most studies on the hedgehog have been done on captive animals (e.g. Herter 1938, Lindeman 1951, Poduschka 1977) and only a few on free living populations (Morris 1969, Brockie 1974, Parkes 1975, Reeve 1982). The latter studies concern mainly home range, territoriality and the solitary habits of the hedgehogs. Their mating system is suggested to be promiscuous but no examination based on data is available (Reeve 1982).

The aim of this study was to examine the mating system and social organization of hedgehogs from data on mating behaviour, movement activity, and the distribution of hedgehogs during and outside the mating season.

STUDY AREA

The study was carried out in a small village (Revingeby) in Scania, southern Sweden. The village covers about 50 hectares and is surrounded by abandoned arable land. The houses have gardens with lawns and bushes along the boundaries. The village also contains four small groves with coniferous and deciduous trees and three large public lawns. Parts of the village are abandoned arable land.

METHODS

The hedgehogs were caught by hand at night with the aid of a powerful torch. Each animal was sexed, weighed and marked with a numbered clip in each ear. Twenty hedgehogs (10 males, 10 females) were provided with radio transmitters. The transmitters, weighing about 20 grams, were cemented on the rear part of the back, where the spines had been cut down in a small area. A portable receiver (27 MHz) was used and the signals were obtained within a radius of 75

to 100 m on the average. Two to five individuals were tracked simultaneously, roughly between 1900 and 0500 and, in some cases, single animals were tracked continuously during the night or during 24 hours. When tracking a single individual, a radio location was taken at least every 15th minute. In other cases, locations were taken with 30-45 minutes interval. The animals were followed as closely as possible without disturbing them. The average number of radio fixes per night was 15. For each individual and night, a movement activity index was calculated as the sum of the straight-line distances between consecutive radio fixes per 15 minutes tracking time. There was no statistical difference between movement indices based on animals tracked singly or on several animals tracked simultaneously (t-test, all cases, $p > 0.1$). Only animals at least two years (i.e. animals living in their third summer or more) were used when analysing mating behaviour and associated movements. Two of the tracked animals were subadults. The results from these were used only to calculate the duration of nightly movement activity.

RESULTS

Mating season and activity

The hibernation period of the hedgehogs in the study area lasted from September to the end of April. Soon after arousal the hedgehogs became sexually active. The main mating period lasted from the middle of May to the middle of July and mating activity peaked during the latter part of May and the earlier part of June (Fig. 1). From the middle of June, mating activity decreased markedly and in August no mating attempts were recorded.

During the mating period, individual males made mating attempts with several females, in some cases during the same night (mating attempt/male tracking night, $\bar{x} = 1.15 \pm 0.88$, range 0 - 4, $n = 35$ tracking nights) and individual females were courted by several males (mating attempt/female tracking night, $\bar{x} = 1.13 \pm 1.39$ (SD), range 0 - 5, $n = 24$ tracking nights). A total of 24 occasions of agonistic interactions were observed in 1977 and 1978. Most of them occurred during the mating period (19 encounters during 63 tracking nights) and a few during the post-mating period (5 encounters during 87 tracking nights) ($\chi^2 = 16.2$, $p < 0.001$, $df = 1$). Males were more frequently involved in agonistic encounters than females (19 encounters during 83 tracking nights for males and 5 encounters during 67 tracking nights for females) ($\chi^2 = 6.6$, $p = 0.01$, $df = 1$). There was, however, no statistical difference between intra-male and intra-female interactions during mating season (male x male: 15 encounters during 42 tracking nights; female x female: 4 encounters during 21 tracking nights) ($\chi^2 = 1.84$, $p = 0.17$, $df = 1$).

Mating index

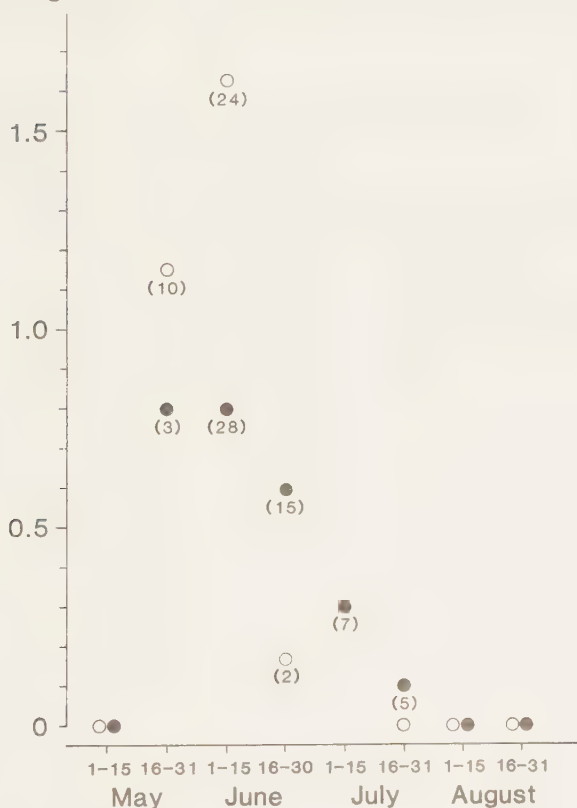


Fig. 1. Mating period of hedgehogs in southern Sweden as indicated by calculated mating indices. A mating index (m_1 , filled symbols) based on hand-capture results from 1976 was calculated according to the formula:

$$m_1 = \frac{N_m \times N_n}{N_c}$$

where N_m is the number of observed mating attempts (36 observations), N_n is the number of capturing nights (63 nights) and N_c is the number of captures (618). Mating indices based on telemetry (data from 1977-1979, open symbols) were calculated according to the formula:

$$m_t = \frac{N_m}{n_i}$$

where N_m is the number of mating attempts (58) and n_i is the sum of radio tracking nights over all individuals (191). The number of matings observed each month is given in parenthesis.

Male-male interactions over a female were observed on six occasions. In all cases one of the males was forced away from the courted female.

Movement activity

Radio tracked hedgehogs were continuously active throughout the nights. The nocturnal activity lasted on average 8.5 hours. In both males and females, there was a tendency for longer activity periods during the post-mating season compared with the mating season (Tab. 1). Females tended to have longer activity periods than males but again the difference was not significant.

Movement intensity was measured as distances per 15 minutes travelled by radio tracked hedgehogs. In June, males showed high movement activity i.e. on average 52 ± 18.3 m (SD). The value significantly decreased in July (36 ± 12.3 , $n = 28$) (t-test, $p < 0.01$) and further so in August and September (Fig. 2). For females radio tracked in June, movement index (23 ± 10.1 , $n = 21$) was smaller than for males (t-test, $p < 0.001$, $df = 8$, $t = 6.27$). In August and September females and males showed similar movement activities (Fig. 2).

Calculated from the movement activity index (m/15 min.) and the average duration of nocturnal activity (Tab. 1), the average straight-line distances covered by males (6 individuals) in June (mating period) was 1761 meter per night. For females (4 individuals) the corresponding figure was 782 m, i.e. less than half the distance covered by males. In August (post-mating period)

TABLE 1

Duration (hours) of nightly movement activity of female and male hedgehogs radio-tracked during the mating season (May 15th to July 15th) and during the post-mating season (July 16th to August 25th). No differences were found between males and females within or between seasons (t-test, $p > 0.05$ in all cases). The number of individual tracking nights are given in parenthesis.

	Mating season	Post-mating season
♂♂	7.7 ± 1.35 (16)	9.0 ± 1.17 (3)
♀♀	8.6 ± 1.66 (12)	9.3 ± 1.79 (6)
♂♂	8.2 ± 1.42 (28)	9.2 ± 1.54 (9)

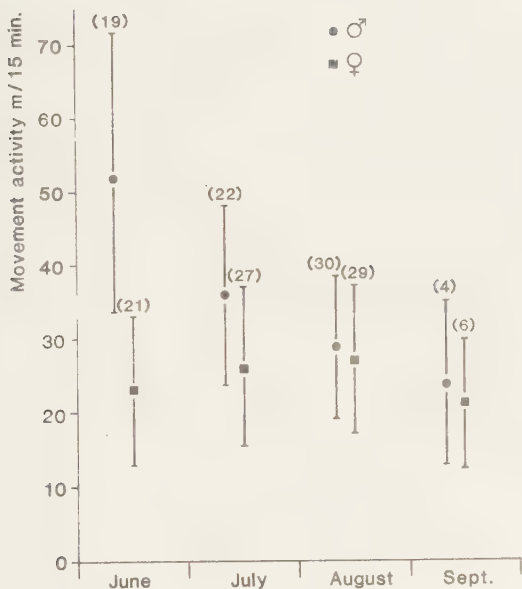


Fig. 2. Movement activity of radio tracked adult male and female hedgehogs during June to September. The movement activity was measured as the straightline distances between consecutive radio locations, recalculated to meter/15 minutes. Nights with mating attempts lasting more than 1 hour were excluded. The figures in parenthesis denote the number of tracking nights and vertical lines denote standard deviation.

the average distances travelled by males decreased considerably, i.e. from 1761 to 1013 m. Females on the other hand increased the movements; average figures increased from 782 to 972 (see also Fig. 4b). Thus, during the post-mating period males and females travelled distances of similar length. Including circular and other not straight-forward movements, as it appears from the continuously radio tracked individuals (Figs 3 and 4), the distance moved by an individual hedgehog probably was twice the straight-line distance.

Distribution of home ranges

The home ranges of individual hedgehogs of the same and opposite sex greatly overlapped (Fig. 5a and b). Females generally had smaller home ranges than males (Paper IV); one male's home range encircled the home ranges of all other tracked hedgehogs except a part of one female's range (Fig. 5a). In addition to the tracked animals there were another 40 hedgehogs in the population (Paper II).

DISCUSSION

Spatial organization

As most insectivores, hedgehogs are solitary animals, forming temporary associations only between the sexes during the mating period and between the female and her young (Eisenberg 1966, Brockie 1974, Kristiansson own obs.).

a



b



0 100 m

The hedgehogs did not show any territorial behaviour neither within nor outside the mating period. They were never seen to patrol any boundaries nor to show any overt aggression over an area, and male and female home ranges' greatly overlapped (Fig. 5). Obviously, territoriality, implying defence of an area, did not occur in the studied hedgehog population. Overlapping home ranges and absence of territorial defence have been observed also in other studies on hedgehogs (Brockie 1974, Parkes 1975).

Ecological factors, such as the temporal and spatial distribution of food resources, are important in shaping mating systems and spacing behaviour (Krebs and Davies 1978, Wittenberger 1981). I shall discuss some of the effects of these factors on the hedgehogs' behaviour.

Hedgehogs feed mainly on invertebrates such as earthworms, insects and snails which occur as a patchy and/or diffused food resource. The availability of earthworms is spatially and temporally heterogeneous, influenced by habitat structure and microclimate condition (Kruuk 1978, MacDonald 1980). In the study area, this food resource was occasionally superabundant.

During the post-mating period, hedgehogs were occupied exclusively with food gathering (Kristiansson own obs.). Territorial behaviour evolves, when the benefit of exclusive use exceeds the cost of defence (Brown 1964). The unpredictable and dispersed food resource forces the hedgehogs to move around in search of these patches. Considering the mating period, the females move around independently of each other in an erratic and unpredictable way (Reeve 1982, this study). This in turn means that during the mating period, the location of the females is unpredictable to the males as are the food resource.

Mitani and Rodman (1979) have attempted to quantify economic defendability in primates. To maintain a territory, the individuals must encounter the perimeter of their range frequently enough to monitor potential intruders. Based on this assumption, they used as an index of defendability the ratio of day-range length to home range area: the higher the index the more defendable is the territory. They found that in all populations with indices of defendability less than one the individuals were non-territorial. A few non-territorial

Fig. 3 (a-b). Nightly movements of an adult male (493) and an adult female (468) hedgehog radio-tracked during the mating season. The male (3a) was tracked eight nights during 12th June - 6th July, 1977. The male travelled on average 2300 m per night with a maximum value of 3500 m. Home range estimate based on 420 radio fixes was 65.7 ha. Two nightly movements (solid and broken lines) are illustrated. Radio fixes (filled circles) outside these routes are places visited during the movements other nights. Stars denote nests. The female (3b) was tracked for five nights during June 13th to July 4th, 1977. Nightly movements were on average 785 m. Home range estimate based on 241 fixes was 19.5 ha. One night excursion is illustrated. Dots outside the route denote radio fixes obtained during other nights.



0 100 m



Fig. 4. Nightly movements of an adult male (720) and an adult female (514) hedgehog radio tracked outside the mating season. Filled circles denote radio fixes. Only some radio fixes are presented on the map. Solid lines show the approximative movement of the tracked individuals during one night. The male (4a) was tracked 18 nights during July 16th - August 23rd, 1979. Mean length moved per night was 1200 m. Size of home range was 19.2 ha, based on 442 radio fixes. The female (4b) was tracked during July 21st to September 9th. Mean length moved was 810 m and home range size 27.5 ha was based on 338 radio fixes. May 29th to June 21st, 1978. Home range estimate was 14.3 ha based on 135 radio fixes. For comparison movements and home range size of the female are shown also for the mating period. The female (4c) was tracked from May 29th to June 21st. Home range estimate was 14.3 ha, based on 135 radio fixes.

populations had indices above one. Two of these were highly insectivorous species, which had indices of 2.3 and 3.4. During the mating period, male hedgehogs had an index of defendability of 2.3 and females 1.6. Post-mating indices for both sexes were estimated to be around 1.6. These figures indicate that hedgehogs have the potential of being territorial. Although path length per se may not affect defendability, properties of food dispersion that constrain daily ranging pattern will be important (Mitani and Rodman 1979). They explained the absence of territoriality in some mobile species by arguing that

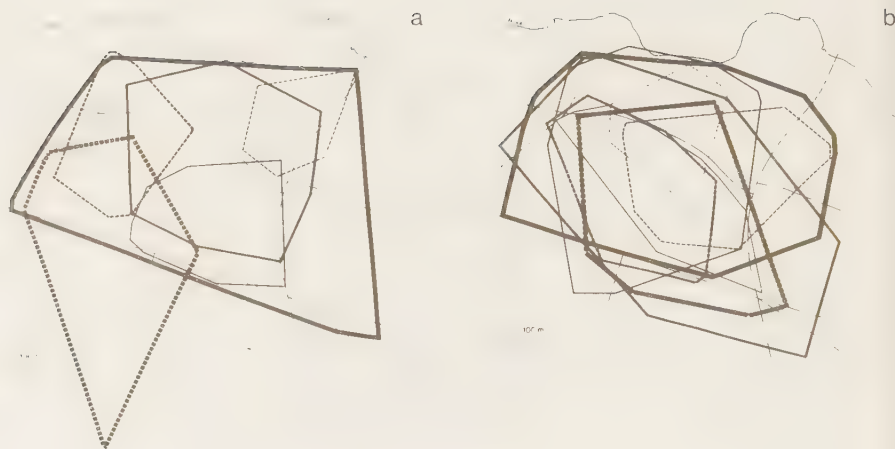


Fig. 5. Distribution of male (solid line) and female (broken line) yearly home ranges, determined by radio-tracking in 1977 (5a) and in 1978 (5b). Captures by hand were added if they changed size and shape of home range. Home ranges of three adult males and three females in 1977 (5a) and home ranges of four adult males and five females and one subadult male in 1978 (5b) are illustrated.

the primary condition (i.e. resource limitation) for the evolution of territoriality (Brown 1964) is absent. Alternatively, some properties of resource dispersion might reduce defendability.

Several factors make territoriality unlikely to occur among male hedgehogs. A territorial male hedgehog should maintain a monopolized area with adequate numbers of food patches and/or other resources to attract females. The distribution of earthworms will promote an irregular boarder line as the territory has to cover a variety of habitats to ensure worm availability. The defence of such a territory is difficult. The females are unpredictable in location due to the patchy and heterogeneous (unpredictable) food resources. The mating ritual may take several hours before mating takes place. If a territorial male tries to ward off and fight every intruding male he discovers, there will be less time to search for and mate with females. A territorial male must also face the risk of being forced away from females that he is courting. It is not uncommon for a female to experience two or three pseudo-pregnancies after mating, i.e. a mating does not necessarily result in pregnancy. Therefore, I argue, the cost of territorial defence is higher than the benefit both during the mating period and the post-mating period or, in other terms, the cost associated with territorial defence is higher than that of strict searching behaviour.

Females showed the same movement activity throughout summer and autumn, and both sexes had a similar movement activity in the post-mating season (Fig. 2). This activity appeared to be devoted exclusively to feeding. In comparison, the males' extensive movements during the mating season (Figs 2, 3, and 4) reflect their efforts when searching for females (Fig. 1). Male hedgehogs lost weight (about 10 %) during the mating season from May to June, while females did not (Paper VI). The weight loss of the males was their cost of searching for females. The obtained figures on length of movements and speed during the mating season are similar to those reported from Britain (Reeve 1982). But in the British study no seasonal change in the hedgehogs' activity was observed.

Generally, the aggression level was low but increased in the mating season, when males were seen to defend females, indicating male-male competition over females. Brockie (1974) observed fightings only at matings and most of my observations were from that period; only a few fights were observed during the post-mating period. Fights over natural food resources were never recorded and hedgehogs were seen foraging close together without any detectable aggression. These results conform with observations from England and New Zealand (Morris 1969, Brockie 1974, Parkes 1975).

Mating system

In general, if only the female lavish parental care and if the probability of her finding another male is high (e.g. when the mating season is long and the female oestrus is asynchronous), then promiscuity will be the males' best strategy (Rubenstein 1980). What polygynous system that develops depends on whether conditions are such that the net reproductive success associated with e.g. guarding females is higher than that associated with searching and strictly promiscuous behaviour (Rubenstein 1980).

Mate guarding in hedgehogs occurred only in connection with courting and mating. Continuous guarding and following were not observed. When the females are dispersed, males attempt to establish dominance via contests and acquire mates largely by virtue of their status and searching ability (Rubenstein 1980). The solitary habits of a female hedgehog render it difficult for a male to follow and guard her longer than it takes for the courting and mating itself, i.e. one night or less. If the male tries to guard her longer, he faces the aggression of the female with a risk of injury and the difficulty of finding the mate successive night(s). Further, there is always a risk of being forced away by another male and finally, the mating might be sterile. In comparison with searching behaviour, a male behaviour devoted to guard a single female would be disadvantageous due to the long time expended on one female and the loss of mating opportunities with other females.

There are no reports on hierarchies among free-living hedgehogs, though this has been observed in captivity (Lindemann 1954, Dimelow 1963). The level of aggression is low, and therefore, data on aggression are meagre. However, I suggest, that hedgehogs establish dominance relationship from case to case with body size as cue, and that fights occur when the assessment fails.

The males' searching behaviour during the mating season, can be explained as a strategy to maximize the number of matings which results in overlapping home ranges. This mating system could be characterized as overlapping promiscuity (Wittenberger 1979). Promiscuity, however, does not imply random mating. In the hedgehog, aggressive behaviour is shown also by the female during the mating ritual (Brockie 1974, Kristiansson own obs.). This aggression might be to test the quality of the male, and could be a cue to the male of the female's receptivity.

In conclusion, I argue that the mating system of the hedgehog is a case of overlapping promiscuity governed by the temporal and spatial dispersion of food resources and the solitary habits, giving the searching and strictly promiscuous behaviour an advantage over other alternatives.

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Paper VI

Body weight changes in the European hedgehog

ABSTRACT

Growth and changes in body weight of hedgehogs over the year were investigated in a population examined by capture-recapture in southern Sweden. Weight data are related to activities to get an understanding of the energetic demands put on the hedgehogs. Both juvenile and subadult individuals increased their weight linearly. There were no differences between juvenile male and juvenile female body weight. Both sexes increased their weight by about 210 %. Subadult males were heavier than subadult females. Both categories more than doubled their body weight from spring to autumn. Adult males which were heavier than adult females decreased in weight during the mating period but increased considerably afterwards. Adult females did not loose weight during the mating period. They increased their weight after the mating period, although the increase was much less and started later in the post-mating period than for the males. In terms of energy demand during the non-hibernation period, male adult hedgehogs appeared to experience hardest strain during the mating period due to the male's searching behaviour after females, whereas adult females face hardest strain during the post-mating period due to pregnancy, lactation and food provisioning. The hibernation period is a bottle neck for the population. The weight loss during this period was estimated to be around 25-40 % of the weight in the autumn, but varied considerably between individuals.

INTRODUCTION

In mammals, growth is a continuous process. Preweaning growth rate is primarily influenced by maternal support, whereas postweaning growth is dependent upon the individual's genetic make up, environmental conditions, and the individual's experience (Phillips 1981). The hedgehog is a hibernating species occurring in many countries and at different climatic conditions. One important characteristic of a hibernating mammal is that important activities such as breeding and rearing young, foraging for maintenance and fat storing for the hibernation all have to be done in a relatively short period. This matter causes the hibernator to accelerate the course of many biological processes (Kalabukhov 1960). Hedgehog populations in different areas experience different climatic conditions which may result in different length of the season devoted to activities and the allocation of energy to reproductive and nonreproductive activities might differ in different areas. From a hibernation study, Kristoffersson and Soivio (1967) suggested that hedgehogs from different areas were physiologically adapted to the prevalent environmental conditions.

In this paper I report on growth and changes in body weight of hedgehogs in southern Sweden over the year. These data are related to the activities of the hedgehogs to get an understanding of the energetic demands put on male and female hedgehogs over the year.

STUDY AREA

The study was carried out in a small village (Revingeby) in Scania, southern Sweden. The village covers about 50 hectares and is surrounded by abandoned arable land. The houses have gardens with lawns and bushes along the boundaries between the gardens. The village also contains four small groves with coniferous and deciduous trees and three large public lawns. Part of the village is abandoned arable land.

METHODS

The hedgehogs were caught by hand at night with the aid of a powerful torch. Each animal was sexed, weighed and marked with a numbered clip in each ear. The hedgehogs were classified as juveniles from birth to the first hibernation, and as subadults during the next summer until the second hibernation. Animals living in their third summer or more were called adults.

Linear regression curves were used to calculate growth rate using pooled

data from the years 1972 to 1978. Regression lines were calculated for two periods, i.e. from April to June (mating period) and from July to September (post-mating period).

RESULTS

The juveniles' body weight increased linearly from about 280 g in August to about 600 g in October, i.e., an increase of about 210 % in two months (Fig. 1). There was no difference in body weight and growth rate of juvenile males and females (males: $y = 7.9x + 845$, females: $y = 7.7x + 837$).

Subadult males and females increased their body weight considerably from spring to autumn in their second year (Fig. 2). Subadult males more than doubled their weight, from 500 g in May to 1130 g in September as did subadult females from 530 g in May to 1110 g in September (Fig. 2). Except in September before the start of hibernation, subadult males were significantly heavier than subadult females. In August the subadults attained the adults' spring body weight (Figs 2 and 3). During the mating period the increase in body weight of subadult males ($y = 3.5x + 479$) was less than that of female subadults ($y = 4.5x + 326$) (test for equality of slopes, $p < 0.001$, Bailey 1976). However, in the post-mating period the weight increase of the two sexes was similar (males: $y = 5.3x + 262$, females: $y = 5.1x + 180$) (test for equality of slopes, $p > 0.1$). For both subadult males and subadult females the increase in body weight during the post-mating period was higher than during the mating period (test for equality of slopes, males: $p < 0.001$, females: $0.01 < p < 0.05$).

The body weight of the adult males decreased by about 10 % from May (955 g) to June (870 g) (mating period) but increased considerably from June to September (from 870 g to 1410 g) (Fig. 3). The weight losses of the adult males during the mating period were on average 1.9 g night^{-1} ($y = 1056 - 1.9x$) and the increase in weight in the post-mating period was 5.5 g night^{-1} ($y = 5.5x + 491$). Except for June and July, the adult males were significantly heavier than the adult females (Fig. 3). In all months, the adult males' body weight exceeded that of the subadult males (Fig. 2 and 3; t-test $p < 0.001$ in all cases).

When activity started in May, the adult females' weight was about 830 g (Fig. 3). The weight increased slightly to June (870 g) and markedly in July (period of pregnancy) to about 1000 g. Data indicated a slight decrease from July to August but again an increase to about 1060 g in September. Adult females were heavier than subadult females in May, June and July but not in September (t-test May, June and July $p < 0.001$; August $0.05 < p < 0.1$, September

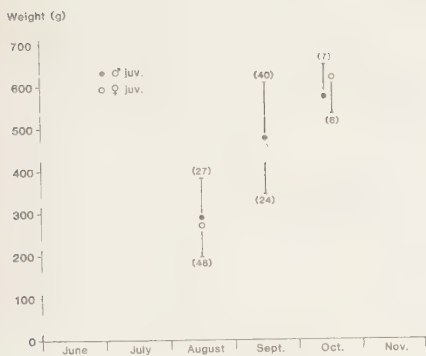


Fig. 1. Mean body weight (g) of juvenile males (filled circles) and juvenile females (open circles). Standard deviation is indicated by vertical lines. Juveniles were initially captured in August and were active throughout October. Number of animals (pooled data from the years 1972 to 1978) is given in parenthesis.



Fig. 2. Changes in mean body weight (g) of subadult males (filled circles) and subadult females (open circles). Standard deviation is indicated by vertical lines. The number of animals (pooled data from 1973 to 1978) is given in parenthesis. Males started activity in the middle of April whereas females became active not until early in May. Both sexes ended activity in September. Significant differences (t-test) between the sexes' weights are denoted.

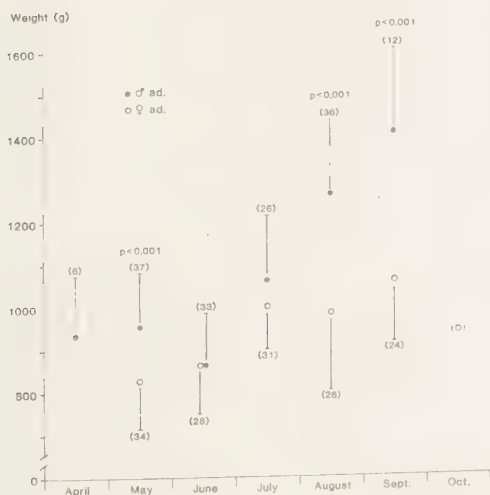


Fig. 3. Changes in mean body weight (g) of adult males (filled circles) and adult females (open circles) during their period of activity (April-October). Standard deviation is given by vertical lines. Number of animals (pooled data from 1973 to 1978) is given in parenthesis. Significant differences (t-test) between the sexes' weights are denoted.

$p > 0.1$). For adult females, growth rate could not be obtained for the mating period ($y = 0.9x + 792$, $t = 1.7$, $df = 167$, $0.05 > p > 0.1$). In the post-mating period, however, growth rate was calculated from data obtained in August and September. Their growth rate ($y = 2.1x + 676$) was less than for the adult males.

Rate of weight loss during the hibernation period was estimated from the adjusted body weights of individual hedgehogs when entering and leaving the hibernation (Tab. 1). Adjusted body weight for each individual was calculated from regression equations using weight data from last captures in autumn and first capture in spring as starting points. For all categories weight losses during hibernation were considerable, about 25 - 40 % of the weight in autumn (Tab. 1). The weight loss varied considerably between individuals. Data indicated highest losses in juvenile females and lowest in adult females and juvenile males ($p < 0.05$) (Tab. 1). For other categories showing intermediate values there were no statistically significant differences.

TABLE 1

Mean adjusted body weight of hedgehogs prior to and after hibernation. For each adult and subadult individual, weights were calculated from regression equations (see text) to 1st of May and 1st of October. Juvenile body weight was calculated to the 15th of October. For adult females, the regression equation for the mating period (which was used to calculate the weight on the 1st of May) was not significantly correlated with capture date (found to lie between 0.05 and 0.1). The equation was, however, applied to adjust for the effect of captures at different dates. t-test for correlated means was used (in all cases $p < 0.05$). Student-Newman-Keuls test of set of means was used to test the differences in proportions of weight decrease. Angular transformation of proportions was used to ensure normal distribution. The solid line connects groups where the differences were not statistically significant at the 0.05 level. Pooled data from the years 1972 to 1978 was used.

Group	Adjusted mean body weight (g) $\bar{x} \pm SD$ Prior to hibernation	After hibernation	weight decrease %
adult male	1566 $\pm$ 208.6(12)	1055 $\pm$ 177.1(12)	32.6
adult female	1108 $\pm$ 110.7(18)	842 $\pm$ 130.0(18)	24.0
subadult male	1321 $\pm$ 157.2(18)	948 $\pm$ 173.0(18)	28.2
subadult female	1102 $\pm$ 165.8(6)	778 $\pm$ 98.2(6)	29.4
Juvenile male	717 $\pm$ 104.9(26)	540 $\pm$ 110.2(26)	24.7
juvenile female	685 $\pm$ 101.7(27)	414 $\pm$ 76.2(27)	39.6

ad.females	juv.males	subad.males	subad.females	ad.males	juv.females
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DISCUSSION

In the study area, hibernation lasted for about 210 days. During the remaining 155 days of the year the hedgehogs have to complete mating, and mated females should pass pregnancy and lactation. Further, the young must have time enough to grow up and, as the nonjuveniles, enough time to store fat to survive the winter. This imposes a time (and energy) constraint on the hedgehogs which varies in different regions and environments. The period of activity can be divided into the mating period which begins just after hibernation, and the post-mating period which for adult males means fat storing, and for adult females pregnancy and lactation in addition to fat storing.

It is difficult to compare body weight data from other studies with those obtained in my study mainly because age grouping of the animals differs and because the sexes have not been separated in some cases. Also, the seasonal changes of body weight make comparisons difficult. It appears, however, that the hedgehogs in my study area are considerably larger than those on the continent and on New Zealand. On New Zealand, the mean body weight was 640 g both for males and females (subadults and adults together) as reported by Brockie (1974) and about 700 g in another study (Parkes 1975). The average weight for adults in England was 700 g both for males and females (Morris in Brockie 1974). Hedgehogs from my study area were also heavier than hedgehogs from Czechoslovakia in the corresponding age groups (Hrabe 1975). Hedgehogs from Germany, however, seem to be as large as Southern Swedish hedgehogs, (Herter 1938).

The adult males lost weight during the mating period. There appears to be several causes for the decrease. An adult male covers in his search for females a distance almost twice as long as that during the post-mating period (Paper V). Activity is mainly devoted to mating and relatively little to foraging (Paper V, own obs.). Metabolic rate for males (and also for females) is about 20 % higher during the mating period than during the post-mating period (Tähti 1978). Obviously, mating behaviour is energy consuming. This suggests that adult males in bad condition should have more difficulties surviving the summer than hedgehogs in good condition.

During the post-mating period, the adult males increased their weight by about 50 % each month (Fig. 3), due to the fat deposition for the hibernation (Herter 1933, Morris 1969, Brockie 1974). In a laboratory study, Kristoffersson and Suomalainen (1964) found that hedgehogs under ideal conditions were capable of increasing their body weight by about 60 % within one month.

During the mating period, adult females increased slightly in weight (Fig. 3). This might partly be due to the fact that some females become pregnant early in the season. In comparison with adult males, more foraging activity

was observed in females (own obs.). For adult females, it is difficult to calculate the weight increase during the post-mating period. During this period, many females are pregnant which may to some degree conceal fat deposition. However, a minimum increase in body weight of about 30 % appears from spring to autumn (Fig. 3).

For adult females, in contrast to adult males, the post-mating period is a time of great food demands connected with pregnancy and food provisioning not only for themselves but also for the young via milk production. This means that females rearing young store less fat at that time. For females, there might be a conflict between giving the young food support as long as possible and thus increasing their chances to survive, and the need for the female to deposit fat to secure her own survival the next winter. In terms of energy supply adult females face hardest strain during the post-mating period whereas male hedgehogs seem to experience hardest strain during the mating period.

In juveniles and subadults, increasing the body weight is a combination of growth and deposition of fat. They both have to deposit as much fat as possible to enhance their chance of survival during hibernation, and, for the subadults to grow as fast as possible to reach adult body weight which occurs in August in their second year.

Subadult males were seen displaying mating behaviour (own obs.). Results from England indicate that subadult males have lower movement activity than adult males (Reeve 1982). In this study, the subadult males did not decrease in weight during the mating period as did the adult males, which might be due to lower mating activity in the subadults than in the adults. In England, female subadults were found to be pregnant as frequently as the adult females (Morris 1969). In this study, however, no subadult females were found pregnant, showing that subadult females generally do not breed in Sweden. The same result was obtained in another study from southern Sweden (Löfqvist pers. comm.). Obviously, subadult female hedgehogs in southern Sweden postpone their first reproduction to their third summer.

The winter period (the hibernation period) is a bottle neck for the hedgehogs. In this study, on average 33 per cent of the hedgehogs (juveniles and nonjuveniles) disappeared from autumn to spring (Paper II). Bodyweight as an index of fat storage was correlated with winter survival in juvenile and subadult males but not in other categories (Paper VI). However, several studies show that substantial weight losses occur over the winter indicating the importance of fat storage. In a laboratory study, hedgehogs from Finland lost about 40-50 % of the initial weight after 160-170 days of hibernation (Kristoffersson and Suomalainen 1964, Kristoffersson and Soivio 1967). Of wild-caught hedgehogs in England male individuals lost about 18 % and females about 39 % of their body weight over the winter (Morris 1969). The estimated weight

losses in my study varied between 20 and 40 % (Tab. 1).

In New Zealand with long summers, hedgehogs produce two to three litters per year, and mild winters provide possibilities for weight gains even during this period (Brockie 1974). Weather conditions may influence the number of animals hibernating. Brockie (1974) found that in a warm winter about 21 % of the population in autumn hibernated, but in a severe winter 63 % of the animals hibernated. In England, the summer is longer than in Sweden which gives some females a chance of producing a second litter. In Sweden no second litters are known. These results indicate a considerable plasticity of hedgehogs in relation to environmental conditions. The large body size and high body weight of hedgehogs in Sweden can be seen as an adaptation to survive a long and severe winter. Also, the postponing of the first litter which permits the females to grow and store fat, unhindered by pregnancy and lactation, can be explained in the same way.

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